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A Monographic Study of the Neotropical Vine Snake, Oxybelis Aeneus (Wagler).

Edmund Davis Keiser Jr
Louisiana State University and Agricultural & Mechanical College

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A MONOGRAPHIC STUDY OF THE NEOTROPICAL VINE SNAKE,

Oxybelis aeneus (Wagler)

A Dissertation

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ABSTRACT

The nomenclatural history of the vine snake Oxybelis aeneus (Wagler) is reviewed. The name Dryinus aeneus Wagler, 1824, is given priority over Coluber acuminatus Wied, 1824, primarily on the basis of a reference to the volume containing Wagler's description in a March, 1824 publication of Spix and Martius. All synonymized species are discussed and the present locations of the holotypes are given. The holotype of Dryinus auratus Bell is believed to be lost.

Analyses of geographic, ontogenetic, sexual, and individual variation are presented for scutellation, head and body measurements, dentition, certain cranial bones, hemipenes, and color pattern. Bogert and Oliver's (1945) concept of two subspecies, O. aeneus aeneus and O. aeneus auratus, based on the relative proportions of eye diameter and internasal scale length is examined. The ratio means of these measurements are shown to change clinally with the length of the snout in several parts of the range, and the ratio itself is insufficiently diagnostic in North American and South American populations. Few other

characters examined are geographically unique and most are subject to a high degree of individual variation. No subspecies are recognized.

INTRODUCTION

The vine snake Oxybelis aeneus is a wide-ranging neotropical species that has been taxonomically misunderstood since it was described in 1824. This lack of understanding has resulted in part from the small number of specimens in museum collections, but mostly from the high degree of variability evidenced by population samples of the snakes themselves. The most extensive revision of the species prior to this study has been that of Bogert and Oliver (1945), based on the examination of 96 specimens. In the present study, 1,218 specimens were examined. All type specimens, with the exception of one that appears to be lost, have been seen. Nearly all characters that have been utilized by other workers in ophidian systematics were studied. The resulting data have been analyzed to determine the extent of individual, ontogenetic, sexual, and geographic variation found in this species. I have undertaken this revision with the intention of contributing to the limited knowledge that is available concerning this species and laying the foundation for future studies on the relationships, phylogeny, evolution, and life histories of these and other snakes within the genus. Many of the conclusions derived from this study must be considered tentative and subject to change or modification as additional data are accumulated.

MATERIALS AND METHODS

At the inception of this study, survey letters were sent to 296 universities and museums in 24 countries to ascertain the number of specimens of Oxybelis aeneus available for study. Of the 212 replies received, 156 institutions reported no specimens available, seven had specimens with no data, and 49 reported one or more specimens with locality data. From three to seven additional letters were sent to a number of the institutions failing to respond, but these elicited no replies. I have been able to examine 1,218 specimens from the 45 institutional collections listed below:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
ASDM	Arizona-Sonora Desert Museum
ASU	Arizona State University
BCB	Bryce C. Brown Collection, Strecker Museum, Baylor University
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CM	Carnegie Museum
CUM	University of Colorado Museum
CU	Cornell University
FMNH	Field Museum of Natural History
IHN	Instituto de Historia Natural, Chiapas, Mexico
IRSNB	Institut Royal des Sciences Naturelles de Belgique
JAP	James A. Peters Collection, United States National Museum
LACM	Los Angeles County Museum

LSUMZ	Louisiana State University Museum of Zoology
MAZG	Max Allen's Zoological Gardens, Eldon, Missouri
MCNC	Museo do Ciencias Naturales, Caracas
MCZ	Museum of Comparative Zoology, Harvard
MNB	Museo Nacional do Brasil
MNHN	Museum National D'Histoire Naturelle, Paris
MSU	Michigan State University
NMB	Naturhistorisches Museum Basel (Schweitz)
RNHL	Rijksmuseum Van Natuurlijke Histoire Leiden, Netherlands
SDSNH	San Diego Society of Natural History
SM	Staatliches Museum für Naturkunds in Stuttgart
SNM	Natur-Museum und Forschungs-Institut Senckenberg
SU	Stanford University
TCWC	Texas Cooperative Wildlife Collection
TNHC	University of Texas Natural History Collection
TU	Tulane University
UA	University of Arizona
UAHC	University of Alabama Herpetological Collection
UCMVZ	University of California Museum of Vertebrate Zoology
UCR	Universidad de Costa Rica
UF	University of Florida Collections
UIMNH	University of Illinois Museum of Natural History
UK	University of Kansas Museum of Natural History
UM	University of Miami
UMMZ	University of Michigan Museum of Zoology
UNM	University of New Mexico
USC	University of Southern California
USL	University of Southwestern Louisiana
USNM	United States National Museum
ZMN	Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität zu Berlin
ZSM	Zoologische Staatssammlung Munchen

In addition to the specimens actually examined, Dr. Alphonse R. Hoge generously supplied me with locality and scutellation data on 74 aeneus in the Instituto Butantan collections (IB). The South American distribution map and the tables and discussions on labial, ventral, and caudal counts include Dr. Hoge's data.

Scale counts were made according to the usual practices. Ventrals were counted by the method proposed by Dowling (1951b). The subcaudal count was begun with the most anterior paired scales in contact and the terminal spike was not included. Twenty linear measurements were made on approximately 200 snakes, seventeen on about 400 snakes, and fourteen on the greater number of those examined. Measurements on the head scales and head were made with vernier calipers under a dissecting microscope as follows: greatest width (w), height (h) and length (l) of the rostral (R); greatest length of the longest internasal (IN); greatest length of the internasals along their common suture (IN'); greatest combined width of the internasals (INw); greatest length (l) and width (w) of the frontal (F); greatest length of the longest parietal (P); distance of snout protrusion beyond the anterior border of the mental

(Sn); greatest length of the longest first infralabial (IL); maximum length of the anterior chin shield (ACS); maximum length of the posterior chin shield (PCS); greatest horizontal diameter of the orbit (E); head width at the level of the posterior edge of the parietals (Hw); head length from the posterior edge of the parietals to the tip of the rostral (Hl'); head length from the posterior edges of the mandibles to the tip of the rostral (Hl); and length of the snout from the anterior border of the orbit to the tip of the rostral (Sl). Badly dessicated or distorted specimens were not measured. Body length (SV) was measured from the anterior tip of the rostral to the posterior border of the anal plate. Tail length (T) was measured from the posterior edge of the anal plate to the tip of the tail. Only specimens with complete or apparently complete tails are included in discussions and tables involving caudal counts and tail lengths.

The following ratios were determined and analyzed by the RCA Spectra 70 digital computer at the Department of Computer Science, University of Southwestern Louisiana:

rostral width/rostral length	(Rw/Rl)
internasal width/internasal length	(INw/INl)
internasal length/head length	(INl/Hl)
internasal width/head length	(INw/Hl)

prefrontal length/head length	(PF/Hl)
frontal length/head length	(Fl/Hl)
frontal width/frontal length	(Fw/Fl)
parietal length/head length	(P/Hl)
anterior chin shield/posterior chin shield	(ACS/PCS)
snout protrusion/snout length	(Sn/Sl)
eye diameter/snout length	(E/Sl)
eye diameter/head length	(E/Hl)
head length two/head length one	(Hl'/Hl)
tail length/snout-vent length	(T/SV)
snout length/head length	(Sl/Hl)
head length/body length	(Hl/SV)
head width/head length	(Hw/Hl)

The above ratios were analyzed for possible ontogenetic, geographic, and sexually dimorphic differences.

The number of scale rows was determined at three points on the body: approximately one head length behind the posterior angle of the mandibles, at mid-body, and at the level of the last ventral. Dorsal scale reductions were made in the manner suggested by Dowling (1951a).

The right maxillae were removed from 78 specimens to ascertain possible differences in shape and size. Additional maxillae were examined in situ by removing the adhering flesh with a dissecting needle and drying the bones rapidly in a jet of compressed air. Skulls were removed from 31 specimens and cleaned for examination. Five additional skulls were supplied by museums. Tooth counts of the dentigerous bones include the number of empty sockets.

Color notes were made on living and preserved specimens. Particular attention was given to the coloration of the head, throat, body, and tail; and pattern features such as flecks, spots, checks, masks, and stripes.

SYSTEMATIC ACCOUNT

Four species (aeneus, argenteus, brevirostris, and fulgidus) are currently recognized in the genus Oxybelis Wagler. The species, Oxybelis aeneus (Wagler), which is treated herein, has the most complicated nomenclatural history.

Wagler (in Spix, 1824) described Dryinus aeneus from Brazil. During the same year, a preliminary report on the specimens to be described in Prince Maximilian zu Wied's "Beitrage zur Naturgeschichte von Brasilien" appeared in heft 6 of Isis von Oken. In this paper appeared the name C. [=Coluber] acuminatus followed by the common name "Spitzkopfige Peitschennater" and a brief description of the holotype, which includes those features Wied considered diagnostic of the new species. The brief passage is identical to the opening summary of C. acuminatus in Wied's 1825 paper usually cited as the original description. Most workers have overlooked the 1824 paper, although Amaral (1925) and Schmidt and Walter (1943a, 1943b, and 1945) listed it as the primary citation in their synonymies of Oxybelis acuminatus. No author is cited for the Isis von Oken paper and according to James A. Peters (in litt.), the name _acuminatus_ should be cited as "Wied, in _Anonymous_."

Since the names _aeneus_ and _acuminatus_ became available in the same year, the establishment of date priority is essential. Wied's paper appeared in heft 6 of the monthly journal Isis von Oken. Amaral (1925) has dated this paper as June, 1824, and it is likely that the issue appeared at about this time. The title page of the volume in which Wagler's description appeared bears the date 1824 and no month. An early reference to this book appeared in a footnote in Spix and Martius (1824: 163), which stated "Crotalus cascavella. (Spix, Serp. Bras., tab. xxiv.)" Miss B. M. Hurst, Archivist for Longman's Green, and Co., of London, informed me (_in litt_.) that the two volumes of Spix and Martius were both published in March, 1824. It is possible that Spix and Martius footnoted the above reference in anticipation of the future appearance of the book, but this can only be considered conjecture and the date of March, 1824, stands as the earliest reference I have found to the work in which the name _aeneus_ first appeared. Furthermore, a review of this book was published in heft 10 of Isis von Oken, only four issues after that in which the Wied paper appeared. It is very likely that the book appeared several months in advance of the review, but this can only be assumed. Although considerable doubt exists on the exact months of publication for the 1824 papers of both Wied and Wagler, the evidence favors the priority of Wagler's aeneus. Furthermore, this name has been in wide usage for the last 22 years, while the name acuminatus has appeared only occasionally during the same period. Unless evidence to the contrary becomes available, the name aeneus should be retained for nomenclatural stability.

Wied (1825) published a lengthy description of the holotype of his C. [Coluber] acuminatus. Bell (1825) described Dryinus auratus from a shipment of specimens he had received from "Mexico." Dalman (1823) noted that the Dryinus of Merrem was preoccupied by insects and proposed the substitute name Dryophis. Boie (1826) placed Daudin's 1802 Coluber fulgidus in Dalman's Dryophis and the following year (1827: 546) listed "Dryinus aeneus. Spix serp. Bras. oder Col. acuminatus Pr. Max Beitrage T.1. p. 322" as number seven in a list of eight species included under the heading "Dryophis." Wagler (1830) proposed the genus Oxybelis, included aeneus as the only species, and synonymized Bell's auratus and Wied's 1825 acuminatus.

Livr. 14 of Wied's Abbildungen appeared in 1830 and plate number 6 included his *C. acuminatus*. Subsequent authors frequently listed Livr. 14 as the first reference in their synonymies, but failed to include a date. Duméril, Bibron, and Duméril (1854: 819) incorrectly assigned the 1822 date of Livr. 1 to Livr. 14, but nevertheless gave Wagler's 1824 *aeneus* priority over Wied's *acuminatus*. From 1854 through 1960, numerous authors assigned priority to *acuminatus* on the basis of the erroneous 1822 date, despite the fact that Garman (1883), Müller (1927), and Bogert and Oliver (1945) correctly allocated the date of Livr. 14 to the year 1830.

Schlegel (1837) used Bell's *auratus* as *Dryiophis aurata* and placed *aeneus* and *acuminatus* in its synonymy. Duméril, Bibron, and Duméril (1854) continued the use of *Oxybelis* aeneus (Wagler) and synonymized *Dryophis* [=*Dryiophis*] *aurata*, Schlegel and other names previously used for the species. Girard (1854, 1855) described *Dryophis vittatus* from Panama, a form eventually synonymized by Günther (1895). Günther (1858), evidently assuming that Wied's Abbildungen was published before Wagler's 1824 description, used the combination *Dryiophis acuminata* and synonymized the *Oxybelis aeneus* (Wagler) of Duméril, Bibron and Duméril of 1854. Cope (1862) was the first to use the combination Oxybelis acuminatus, though subsequent authors have credited Steindachner (1867) with this arrangement.

From the mid 1800's through the early 1900's nomenclatural chaos predominated as virtually every combination of the generic names Dryophis, Dryiophis, and Oxybelis and the specific epithets acuminatus, acuminata, and aeneus appeared again and again in the literature. The extent of the confusion may be indicated by the existence of at least seven works that contain references to either Dryophis and Oxybelis acuminatus or Oxybelis acuminatus and O. aeneus in the same paper. Boulenger (1896) provided some stimulus for stability when he accepted the erroneous 1822 date for Wied's description and used Cope's combination of Oxybelis acuminatus. Dryophis and Dryiophis were rarely used after 1896. The specific name acuminatus dominated the literature between 1900 and 1945, although a few authors persisted in the use of aeneus. Müller (1927) corrected the date of Wied's Abbildungen Livr. 14 and advocated the priority of aeneus. Despite Müller's paper, acuminatus remained in wide use until Bogert and Oliver (1945) advanced independently derived but identical arguments to synonymize *acuminatus* in favor of *aeneus*. They, as well as Müller, however, overlooked Wied's earlier paper in Isis von Oken. Bogert and Oliver also synonymized *Oxybelis microphthalmus* Barbour and Amaral (1926) and *O. potosiensis* Taylor (1941), and subdivided *aeneus* into the two subspecies, *O. aeneus aeneus* (Wagler) and *O. aeneus auratus* (Bell). Most workers since 1945 have followed their conclusions, although a few (Hall, 1951: 212; Taylor, 1951: 128, 1954: 751, *et seq.*) have expressed some degree of dissatisfaction with that nomenclatural arrangement. Hall (1951) used the name *Oxybelis auratus* (Bell) and on p. 212 noted, "It appears that *auratus* antedates *acuminatus* Wied. The specific and subspecific relationship of Mexican forms is still open to question."

The following chronologically arranged list summarizes the changes in the nomenclature of this species. Only the first appearance of a name or combination is included.

OXYBELIS AENEUS (WAGLER)

Dryinus aeneus Wagler, 1824: 12

Coluber acuminatus Wied, 1824: 667

Dryinus auratus Bell, 1825: 325

Dryophis aeneus, Boie, 1827: 546

Oxybelis aeneus Wagler, 1830: 183

Dryiophis aurata, Schlegel, 1837: 255

Dryophis vittatus Girard, 1854: 226

Dryiophis acuminata, Günther, 1858: 156

Dryophis acuminatus, Cope, 1860: 555

Oxybelis acuminatus, Cope, 1862: 356

Dryiophis acuminatus, Cope, 1871: 204

Dryiophis aeneus, Garman, 1887: 284

Dryophis acuminata, Ferrari-Perez, 1886: 185

Oxybelis acuminata, Cope, 1900: 333

Oxybelis microphthalmus Barbour and Amaral, 1926: 80

Oxybelis fulgidus, Crimmins, 1937: 233

Oxybelis potosiensis Taylor, 1941: 128

Oxybelis aeneus aeneus, Bogert and Oliver, 1945: 381

Oxybelis aeneus auratus, Bogert and Oliver, 1945: 381

Oxybelis auratus, Hall, 1951: 212

Oxybelis accuminatus, Wehekind, 1955: 12

TYPES AND TYPE LOCALITIES

The holotype of *Dryinus aeneus* Wagler is a specimen from the forests adjacent to the river Solimõens near Ega. According to Bogert and Oliver (1945: 389), "Ega" is an older name for the town of Teffé, near the junction of the Rio Teffé and Rio Solimõens, almost in the center of the Brazilian state of Amazonas. Teffé is spelled "Tefé" on maps issued by both the American Geographical Society and the National Geographic Society. Stuart (1963: 108) noted that the type of *Dryinus aeneus* was a specimen in the series 2376 to 2384 of the collections of the Zoologisches Museum, Berlin. The curator, Dr. Günther Peters, kindly loaned me this series for examination. Only two specimens were from Brazil and neither is the specimen described by Wagler. Peters (1960: 533) stated that this type is in the collections of the Munich Museum. Dr. Walter Hellmich searched through the Munich Museum collections and identified ZSM 2645/0 as the holotype of *Dryinus aeneus* Wagler.

Wied's holotype of *Coluber acuminatus* is a specimen from the region of the Espirito Santo River in Brazil. The type was identified by Bogert and Oliver (1945: 390) as No. 3886 in the collections of the American Museum of Natural History.

The *Dryinus auratus* of Bell was described from a shipment of specimens the author had received from "México." Günther (1858: 156) listed 14 specimens of *Dryiophis acuminata* in the collection of the British Museum. The second specimen on the list was recorded as "b. Adult. Brazil? Presented by T. Bell, Esq." After considerable correspondence concerning this subject, I am convinced that the specimen mentioned by Günther was actually the holotype of *auratus* described by Bell. Drs. A. G. C. Grandison and L. C. Stuart (*in litt*.) are also of this opinion. In addition, Dr. Grandison has informed me that Günther's specimen is no longer at the British Museum and has probably been lost. Smith and Taylor (1950: 340) restricted the type locality of *auratus* to the "city and environs" of Tehuantepec, Oaxaca, México. Dr. L. C. Stuart (*in litt*.) stated that it is extremely unlikely that collectors would have been in this area around 1825. Schmidt (1953: 219) restricted the type locality to Sonora, México, despite the fact that Bogert and Oliver (1945: 305) had noted 1851 as the earliest year for which collections were known from the state of Sonora. It is unfortunate that the earliest name for the Mexican populations cannot be assigned to a specific locality and that considerable doubt exists that the type specimen was even from Mexico.

Girard's holotype of Dryophis vittatus is a specimen collected on Taboga Island, Bay of Panama, Panama. The specimen is No. 7315 in the collections of the United States National Museum.

Barbour and Amaral (1926) described Oxybelis microphthalmus from a single specimen collected by S. H. Beattie. The type locality was listed as Calabasas Canon, Santa Cruz County, Arizona. The type is No. 22417 in the collections of the Museum of Comparative Zoology at Harvard University.

Taylor (1941) described Oxybelis potosiensis from a specimen he collected 38 kilometers northwest of Ciudad Maiz, San Luis Potosí, México. The type is No. 25069 in the collections of the University of Illinois Museum of Natural History.

DISTRIBUTION

The vine snake Oxybelis aeneus occurs at low to moderate, and occasionally higher, elevations throughout most of the tropics in the Neotropical realm. Its range extends from southern Arizona, south along the eastern and western coasts of México, across the Isthmus of Tehuantepec, throughout most of Central America and into South America. In the southern continent, aeneus ranges west of the Andes as far south as northern Perú; into the valleys of the Cauca and Magdalena rivers of Colombia; and throughout most of northern South America from the eastern slopes of the Andes to the Atlantic coast. The species extends southward at least to central Bolivia and southeastern Brazil and may occur in portions of Paraguay and northern Argentina. It is known from the Tres Marías Islands west of Nayarit, México; Isla Blanca of northeastern Quintana Roo, México; the Islas de le Bahía of Honduras; Los Blancos of El Salvador; Corn Islands of Nicaragua; Naranjas and the Pearl Islands of Panama; and the Testigos, Aruba, Margarita, Tobago, and Trinidad off the northern coast of Venezuela. These snakes are not found in the peninsula of Baja California.

ARIZONA. Vorhies (1926) was the first to record this species as new to the fauna of the United States. He reported specimens from Tucson and from Calabasas Canyon in Santa Cruz County. The Tucson specimen was later mentioned by Barbour and Amaral (1926), Ditmars (1937), and Wright and Wright (1957). Despite intensive work by numerous collectors in this area, no additional specimens have been found and it is possible that this record is an error. The species is definitely known only from the Upper Sonoran life zone of the arid Pajarito Mountains. Wright and Wright (1957) stated that these snakes were found between 2,000 and 4,000 feet, although Fowlie (1965) considered them rare below 3,000 feet. Detailed descriptions of the Arizona habitat have been given by Campbell (1934), Stebbins (1954, 1966), Wright and Wright (1957), Lowe (1964), and Fowlie (1965). These snakes frequent the brush-covered hillsides and gullies, and the canyon bottoms grown over with sycamore, oak, walnut, thorn trees, and wild grape. Lowe (1964) stated that they are also found among the grasses and reeds at the side of streams and ponds. Fowlie (1965) noted that they have been observed in Calabasas, Walker, and Peña Blanca Canyons.

EASTERN MEXICO. In 1937, Crimmins reported a specimen he considered to be _Oxybelis fulgidus_ from Horsetail Falls "about 35 km south of Monterey [_sic_], Coahuila." Smith and Taylor (1945) relegated Crimmins' _O. fulgidus_ to the synonymy of _Oxybelis acuminatus_ (=_O. aeneus_). Horsetail Falls is actually in Nuevo Leon and Crimmins' record is apparently the northernmost record for eastern México, but I have been unable to locate the specimen. The snake was said to have been collected among boulders in the canyon below the falls. Martin (1958) reported specimens of _aeneus_ that were taken in tall tropical forest and tropical semi-evergreen forest at elevations of 100, 350, and 480 meters in the Gomez Farias region of Tamaulipas. The species also occurs in the thorn and scrub forests to the east of Gomez Farias, and on the coast in the areas around Tampico and Ciudad Veracruz. Kennedy (1965) described a specimen from an area northwest of Lerdo de Tejada, Veracruz, that was taken in the coastal sand dunes. He characterized the locality as having dense but scattered thickets of cactus and scrub vegetation and intervening areas covered by sparse, grassy vegetation often subject to grazing.

WESTERN MEXICO. Bogert and Oliver (1945) discussed specimens from Alamos and Guirocoba, Sonora. Their material from Alamos was taken in short-tree forest of the Subtropical life zone. According to these authors (p. 308), Gentry (1942) described this forest as "A heterogeneous deciduous forest with a strong infusion of tropical elements." This forest lies principally in the Barranca regions and ranges from 1,000 to 3,500 feet above sea level according to Bogert and Oliver. Guirocoba was described as being in the foothills of the Sierra Madre Occidental in an area of semi-arid climate with dry summers. Zweifel and Norris (1955) described the Guirocoba region as an area of tropical deciduous forest and noted that *aeneus* was the third most readily obtained snake in the region.

Fugler and Dixon (1961) reported specimens from Culiacán, Sinaloa, in a region of intensive agriculture on the coastal plain. Croulet (1963) saw an individual in heavy roadside vegetation on the coastal lowlands near San Blas, Nayarit. Duellman (1958) noted that *aeneus* was known from the lowlands of Nayarit, Colima, and Michoacán, and the Balsas Basin, but not on the western plateau. He mentioned one snake that was collected in a tree near Pueblo Juarez, Colima, at an elevation of 1,500 feet in plateau scrub forest that was adjacent to riparian forest. Oliver (1937: 1) reported a specimen from coastal Colima and described the area as follows:

> The first of these is the coastal region, which is characterized by dense vegetation and much humidity. There are numerous swamps and lagoons surrounded by thick hardwood forests, open scattered patches of savanna grassland, and a few arid portions with cacti and other xerophytic plants.

Oliver considered the species rare in Colima. Davis and Dixon (1959) recorded <u>aeneus</u> from the tropical deciduous forests of Guerrero. Davis and Smith (1953: 136) discussed a specimen from Progreso, Morelos, and stated: "The luxuriant vegetation reminds one somewhat of the tropical lowlands near Acapulco, Guerrero."

Duellman (1961) noted that <u>aeneus</u> was common on the seaward slopes of the Michoacán Sierra de Coalcomán in regions of tropical deciduous forest and in oak forest to elevations of 1,700 meters. He mentioned one specimen taken in the gallery forest at 730 meters on the northern slopes of the Sierra de Coalcomán, and four specimens taken at 900 meters on the slopes of the Cordillera Volcánica. He also observed that *aeneus* does not inhabit the lower parts of the Tepalcatepec valley. Duellman (1954) noted the absence of this species on the malpais of Jorullo Volcano and credited this to the lack of suitable habitat. The presence of *aeneus* in the coastal areas of Michoácan and its absence in the Balsas Basin were also mentioned in this paper. Duellman (1958), as previously noted, had listed the species as present in the Balsas Basin, but later (1965b), he noted that it was present in the lowlands and adjacent foothills of the Michoácan Pacific coast but not in the Balsas-Tepalcatepec Basin. In his 1965b paper, Duellman considered *aeneus* to be abundant in the tropical semi-deciduous forest, moderately abundant in the lower elevations of the pine-oak forest, and absent in the fir forest and mesquite-grassland. The localities for two specimens Duellman reported in 1961 (Playa Azul and Punta San Telmo) are described in that paper as being within the Arid Tropical Scrub Forest. Concerning this forest, Duellman (1965b: 656) stated, "Likewise, the absence of extensive arboreal habitat precludes the presence of such species as *Sceloporus melanorhinus*, *Leptophis diplotropis*, and *Oxybelis aeneus*, or greatly restricts their distributions."

Peters (1954) found these snakes in trees and on the ground at various localities on and near the Michoacán coast and noted that this species was the most common snake in the region.

SOUTHERN MEXICO. Smith (1943) reported these snakes from Mt. Guengola and Tehuantepec in Oaxaca. Hartweg and Oliver (1940: 8) described these arid localities as follows:

> The vegetation of the Tehuantepec region consists mainly of spiny scrub and of many varieties of cacti, with a few large trees interspersed. The vegetation on Quiengola mountain differs from that about Tehuantepec mainly by the greater abundance of trees and the consequent shading out of some of the smaller plants on the plains proper. Bromelias are present, but are very scarce. Much of the plains area is given over to grazing and farming; irrigation is used extensively. Large coconut palms are frequently found on the borders of the large farms and along the irrigation ditches. The scarcity of decaying logs is amazing.

Woodbury and Woodbury (1944) reported nine of these snakes that were taken in Oaxaca in arboreal habitats in low second growth timber. Charles M. Bogert (in litt.) found an aeneus on the outskirts of San Felipe Aqua at 5,600 feet in Oaxaca, and told me of another that was taken near or above the 6,000 foot level on Cerro San Felipe. Bogert mentioned that his collectors at Tejocotes had reported this snake as present but very scarce at elevations of 7,600 to 8,000 feet. Gadow (1910) considered the range of Dryophis acuminatus (=Oxybelis aeneus) in México as sea level to 4,000 feet.

Del Toro (1960) has noticed that this species inhabits trees, shrubs, and thickets in Chiapas. Landy, Langebartel, Moll, and Smith (1966) mentioned a specimen that was taken by a fence row of tall plants along a cliff edge bordering a banana grove at Volcán Tacána in southern Chiapas. Duellman (1965a) recorded aeneus from a region of dense scrub forest at an elevation of about 10 meters in Yucatán.

CENTRAL AMERICA. Schmidt (1941) and Neill and Allen (1959) have characterized the climatic climax association of British Honduras as rainforest. The latter authors reported an aeneus that was collected on a dusty road at Mountain Pine Ridge near a camp on Privassion Creek in pine parkland surrounded by rainforest, jungle, and cohune ridge. The elevation at this site was 1,400 feet. Schmidt (1941) reported specimens from several areas including the city of Belize. According to Neill and Allen, the peninsula on which the city is located lies at an elevation of less than 24 inches and the natural cover was once almost entirely mangrove swamp.

Stuart (1935) noted the occurrence of these snakes in the savanna bush west of La Libertad in Petén, Guatemala, and considered them rare in that area. He described the region as follows (p. 15):

> The savanna country of central Petén may be considered as a transition area between the northern sapodilla forest country, and the little known forest region to the south along the Arroyo Subín and the Río Pasión. The bush areas of the savanna country are entirely secondary growth, called '_acahual_' locally.

Stuart described the climate of the region as one of uniformly high temperatures and markedly seasonal rainfall. The open savannas of the region support a vegetation dominated by short grasses, with scattered low, scrubby trees. Clusters of sub-xerophytic trees and shrubs occur in the vicinity of shallow _aguadas_. The bush and savannas are frequently subjected to periodic fires during times of drought. Stuart (1958: 27) reported _aeneus_ from Tikal and Uaxactún in northern El Petén, and stated:

> All individuals from Tikal were secured among the tall grasses, sedges, and hydrophile shrubs that were cut within the _aguada_ as a water conservation measure.

> My experience with this form in Guatemala is rather extensive, and I have always associated it with scrubforest or desert-shrub conditions. At Tikal only the brush of the _aguada_ and possibly some of the scrubbier parts of the _akalchés_ appear to offer suitable habitat for this snake.

Commenting on the presence of _aeneus_ around the _aguada_ at Tikal, Stuart said (p. 11): "I believe they were drawn to this habitat more by the scrubby nature of the vegetation (the normal habitat of this form) than by any affinity for humid conditions." According to Stuart, the Uaxactún-Tikal area is climatically and vegetationally transitional between the drier outer end of the Yucatán Peninsula to the north and the humid base of the Central American foreland to the south. Stuart recognized four herpetofaunal microenvironments within the El Petén scrub forest and considered _aeneus_ to be one of the five species characteristic of the trees and lower tree trunks of the microenvironment he termed the "lower forest story." Duellman (1963) reported _aeneus_ from Chinajá in southern El Petén. He recognized bushes, tree trunks, tree tops, and epiphytes as divisions of the arboreal habitat and considered this snake to be a bush inhabitant with diurnal habits. He noted the presence of rainforest in the Chinajá region, but stated that a limited amount of suitable habitat was available for such forms as Oxybelis aeneus that are more frequently found in open forest of a drier nature. Chinajá lies at an elevation of 140 meters. Stuart (1948) reported a specimen from a cane field at La Primavera in Alta Verapaz, Guatemala. Later (1950), he recognized five life areas in Alta Verapaz and listed aeneus for the Corozo life area (Lower Tropical Zone, 0-600m) and the Coffee life area (Upper Tropical Zone, 600-1,300 m). He noted that all three of the major habitat types in Alta Verapaz (forest, grassland, and aquatic-riparian) are located within each of the five life areas, but emphasized the lack of uniformity in any single habitat throughout the five areas. Stuart (1954a) determined that a chain of dry land environments extends from the Isthmus of Tehuantepec to the xeric Motagua Valley of Guatemala which provides ample subhumid pathways for dispersal eastward into Honduras and southward to lower Central America. This subhumid corridor lies mostly below 1,000 meters and, except for narrow breaks, cuts through the highlands of Chiapas and Guatemala. He points out the absence of mesic species and the presence of wide-ranging xeric types, including Oxybelis aeneus in the corridor. Slevin (1939) noted a specimen from the slopes of Volcán Zunil in Suchitepequez Province, Guatemala, but failed to give details on the habitat. Stuart (1951) listed aeneus as a typical species of the semiarid headwater valleys of the Cuilco, Saleguá, and Negro rivers of southeastern Guatemala and stated (p. 14): "Wherever headwater streams of the Cuilco and Negro river systems can break into the highlands of the Chimaltenangan area, the more tolerant forms of this xeric fauna invade the fringes of the southeastern highlands to considerable elevations." Stuart (1954b) secured a specimen from a patch of dense brushland at 575 m in southeastern Guatemala and termed the species typical of subhumid areas at elevations below 1,000 meters.

In Honduras, aeneus is distributed on both coasts and it probably ranges inland to moderate elevations particularly along river valleys with suitable habitat. Dunn and Emlen (1932: 21) have noted that "Faunistically, Honduras is comparable with Nicaragua." Carr (1950) has outlined a variety of habitats for Honduras, but the available papers on aeneus in this country contain little or nothing on its habitats. Barbour (1928) reported these snakes as very common around Coxen Hole on Ruatan Island.

Mertens (1952) noted that these snakes were difficult to collect, but not rare in El Salvador, and that they should be distributed throughout the entire country. He collected a specimen that was sunning among the flowers of Sclerocarpus about 1 meter off the ground on a street under construction in San Salvador. Numerous Lantana bushes were in the vicinity. Rand (1957) mentioned two specimens collected in El Salvador. One was in a bush near the sea on the island of Los Blancos. The other was found on the north slope of Volcán San Salvador at 500 to 700 meters on a 1917 lava flow. According to Rand, the older, rough lava around the most recent flow supported a dry scrub forest much entangled with brush and vines.

Little published information exists on the habitats occupied by aeneus in Costa Rica. The species occurs on both coasts and ranges into the foothills of the Cordillera Volcánica, Cordillera Central and Cordillera de Talamanca. The coastal populations are probably connected in the low elevations north of the Cordillera Volcánica and in the lower elevations of the highland areas. Heyer (1967) studied herpetofaunal distribution patterns along a 25 km transect through the Cordillera de Tilaran in northern Costa Rica. He defined four herpetofaunal assemblages and noted that _aeneus_ was present in Assemblages I (Tropical Dry Forest and Subtropical Moist Forest Zones), II (Tropical Moist Forest and Lower Subtropical Wet Forest Zones), and III (Upper Subtropical Wet Forest and Subtropical Wet Forest Zones), but not in IV (Tropical Wet Forest Vegetation Zone).

Barbour (1906) reported this species from the savanna of Panama. Bangs (1906) described this area as a low, dry grassy plain with island-like patches of wood. Dunn and Bailey (1939) mentioned a specimen taken from the uplands of the Canal Zone at 1,600 feet. Slevin (1942) reported an _aeneus_ that had been collected from bushes in open pasture land at Bouquete. Sexton, Heatwole, and Knight (1964) found eggs of this species in undisturbed, open, mature forests in the Canclón area of Darién Province, Panama. They described the terrain in this vicinity as flat and sloping upwards towards the west, but interrupted by frequent low hills rising 40 to 100 feet above the flood plains. The Canclón region has pronounced wet and dry seasons and Breder (1946) has noted that the area belongs to Goldman's Arid Lower Tropical Zone

This species is apparently abundant in Panama. Bates

(1928) noted that 308 specimens were turned in for bounty money in the Canal Zone. Dunn (1949) reported 1,440 of these vine snakes in a collection of 11,763 Panamanian snakes turned in for identification between 1933 and 1945. He presented an analysis of species abundance and noted that aeneus made up 19.4, 22.2, 10.9, and 1.9 percent of the total catch from Coclé-Herrera, Sabanas, Chagres, and Darién, respectively. This was the most abundant species in the Sabanas and Chagres collections and second only to Leptodeira rhombifera in the Coclé-Herrera collection.

SOUTH AMERICA. Ruthven (1922) reported these vine snakes from Bolivar at elevations to 800 feet, San Lorenzo, Fundación, Arroyo de Arenas, and San Miguel at 6,000 to 8,000 feet, in the Sierra Nevada de Santa Marta region of Colombia. At Bolivar, Fundación, and Arroyo de Arenas, these snakes were taken in bushes and trees. Ruthven gave a detailed account of several of these localities. Bolivar is a small farm about 100 feet above sea level, in a region of irrigated areas and low, semi-arid woodland, acacias, and cacti. San Lorenzo is an isolated mountain peak northwest of the main Sierra Nevada, but connected to it by a ridge having a minimum elevation of about 5,000 feet. The entire mountain is densely forested, except where it has been cleared for cultivation. Ruthven reported two towns named Fundación in this region and failed to note the one at which the *Oxybelis* was collected. Arroyo de Arenas is a cattle ranch at the edge of the flood plain of the Rio Camarones and lies approximately 500 feet above sea level. The vegetation is described as flood plain forest surrounded by low woodland of the dry forest type, with acacias and cacti being conspicuous. Amaral (1928: 7) submitted an account of additional specimens from the Santa Marta region. One specimen came from what he termed the sand and cactus belt near the Ciénega Desert. A second came from the banana belt of Santa Ana and Aracataca, and a third from the Rio Frio region "anywhere from sea level to the western slopes of the Sierra Nevada." Cope (1899) reported the species from near Bogotá, but Dunn (1944a) believed this record to be in error. Dunn further related that *aeneus* ranged to San Pedro at 2,560 meters in the central Andes and to Sasaima at 1,225 meters in the eastern Andes. Dunn (1944b) stated that this species was very common and abundant throughout most of Colombia at elevations to 1,500 meters, and noted that it ranged to 2,410 meters both in the Cordillera Central and in the Sierra de Santa Marta.

Boulenger (1898: 107) mentioned a specimen from Paramba, Ecuador, and gave the following details on the area:

> _Paramba_, a farm on the W. bank of the River Mira, at 3,500 feet altitude; it is still in the forest region, but the open country commences two or three miles higher up the Mira.

Parker (1938) listed this species as occurring in the Arid Tropical and Subtropical zones of the Catamayo Valley drainage system in the west and the Malacatas Valley drainage system in the eastern part of Ecuador. He noted that the Arid Tropical and Subtropical zone on the western side of the mountains extends up to 6,000 or 7,000 feet and probably links up with the coastal deserts of northern Peru in the Catamayo Valley, and that on the eastern slopes, it extends approximately between 3,000 and 6,000 feet. He reported specimens from the Catamayo Valley at 4,700 feet and from the Malacatos Valley at 5,187 feet. James A. Peters (_in litt._) has informed me that he collected an _aeneus_ at approximately 1,250 meters at a locality west of Santa Isabel in the Ecuadorian province of Azuay.

Little is known concerning the ecology of _Oxybelis aeneus_ in Perú. Cope (1877) reported a specimen from the Chimbote Valley. Boettger (1898) mentioned a specimen from Pacasmayo on the northern coast. Prado and Hoge (1947) gave an account of one from Pucallpa in the valley of the Rio Ucayali, in eastern Perú. John P. O'Neill collected a specimen from a sewer ditch at a small village northwest of Pucallpa. According to O'Neill, the area was once tropical lowland forest, and has now been cleared except for a few forest remnants. Dunn (1923) reported the species at Bellavista in the low broad and arid valley of the Río Marañon of northeastern Perú. Schmidt and Walker (1943a) described a specimen from Chanchamayo, a tropical lowland locality in central Perú at the headwaters of the Río Perene in the Department of Junin, and another from the Department of Madre de Dios in southeastern Perú. According to these authors, Madre de Dios is mostly tropical lowland that is bordered by mountains in the south. Schmidt and Walker (1943b) noted that this species occurs in coastal Peru, but had no specimens at their disposal. They explained the presence of certain non-endemic species along the north Peruvian coast as follows (p. 298):

> The Hispanic Map published by the American Geographical Society indicates that there are three passes over the western Cordillera near the Ecuadorean border of Peru somewhat below 10,000 feet elevation, and various passes between coastal Piura and Lambayeque and Andean Cajamarca at less than 8,000 feet. These passes explain the presence of some non-endemic forms of Amazonian or Ecuadorian origin in the northern part of the coastal area and also throw light on the transgression of certain elements of the Marañon valley. Farther south the passes are at fourteen to sixteen thousand feet, well above the altitude reached by any species of the coastal fauna proper.

Numerous papers have mentioned snakes of this species from various localities in Venezuela, but few have contained ecological information. Fowler (1913) reported specimens from the Orinoco delta region. Schmidt (1932) discussed specimens from Cocollar that were collected at 3,600 feet in the easternmost part of the Venezuelan Andes in the Department of Sucré. Roze (1952) described a specimen from El Junquito, D.F., from the subtropical rainforest between 1800 and 2100 meters. Rohl (1942) noted that these snakes occur in lianas and trees in Venezuela. Meek (1910) and Brongersma (1940) reported this species on Margarita Island. Roze (1964) related that Oxybelis aeneus in Venezuela ranges from xeric to sub-xeric regions at sea level to areas that are relatively humid at 2,000 meters. He noted that the same phenomenon occurs in miniature on Margarita Island where the snake is found in the xeric regions of Boca del Río and also on the humid, higher slopes of Cerro Copey. The species has also been reported on the Testigos Islands by Garman (1887) and Roze (1964). Aleman (1953) presented an account of specimens from the Sierra de Perijá region at the localities of Ayapa (1,000 meters) and Kunana (1,130 meters). Roze (1959) listed the species from the Paria Peninsula and the Curapao power plant in the state of Miranda. The latter locality was described as being on the northern slopes of the Cordillera de la Costa at approximately 1,300 meters. The region was described as humid and covered with dense forests, in some places forming a sort of cloud forest. Lancini (1962) described the Curupao region as being tropical rainforest with rainy and dry seasons and a mean annual temperature varying between 14 and 22 degrees centigrade.

Beebe (1946) reported aeneus to be a common snake in the open jungle and along the rivers in the vicinity of Kartabo, British Guiana. He found the snakes among tree branches and in tall bamboo. Earlier (1925) he had described the Kartabo Tropical Research Station in considerable detail. The station is situated by the Mazaruni River near the junction of the Cuyuni River. He characterized the area as one of low rolling hills, with swamps, moist lowlands, and a littoral flora of numerous mangroves along the tide-affected rivers. The littoral flora abruptly merges into jungle of typical rainforest on the higher ground. Parker (1935) noted this species from the forested areas along the Cuyuni and Mazaruni rivers and mentioned a specimen from the more open and southerly Rupununi Savannah.

In 1824, Wagler described the type of _Dryinus_ _aeneus_ from the forests adjacent to the river Solimõens near Ega. Ega is an older name for Tefé, a town in the state of Amazonas, Brazil. Wagler noted that these snakes always occupy the branches of trees. Amaral (1935) listed this species as common in the woody districts of central and northern Brazil. Schmidt and Inger (1951) reported _aeneus_ from the savannas of Ceará Mirim in Rio Grande do Norte. Hoge (1952) mentioned a collection from the Ilha do Bananal area on the border of the states of Goias and Mato Grosso that contained one of these snakes. He stated that this area is in the zone of fields and thickets that is usually termed tropical savanna.

Dunn (1944a), Smith and Taylor (1945), Beebe (1946), and Cagle (1957, in Blair, et al.) have included Argentina in the range of this species. I have been unable to locate specimens from this country.

Mole (1924) observed these snakes frequenting bushes and trees on the island of Trinidad. Johnson (1946) collected a specimen from Tucker Valley, Trinidad, and described the area as having a wide swampy bottom that has been largely drained and occupied by citrus fruit plantations and patches of jungle. The valley is bounded by steep hillsides. The snake was found climbing a palmetto about four feet above the ground. Oxybelis aeneus is well known on Tobago, and its occurrence there apparently was first reported by Boettger (1898). Schlegel (1837: 256) reported Dryiophis aurata (=Oxybelis aeneus) from Martinique collected by "M. Plee." Duméril, Bibron, and Duméril (1854) and Hallowell (1856) have also listed this specimen as being from Martinique. Barbour (1914) regarded this species as incorrectly recorded from the West Indies.

Locality records for the museum specimens examined, and the Instituto Butantan aeneus are shown in Figures 1 and 2.

CHARACTER ANALYSIS

Morphological characters usually employed in ophidian systematics have been utilized in this study of *Oxybelis aeneus*. When possible, these characters have been analyzed statistically to determine the extent of individual, sexual, and geographical variation within the species. Statistical analyses on all linear measurements were done by the IBM 1620 and RCA Spectra 70 digital computers under the direction of personnel from the University of Southwestern Louisiana Computer Science Department. Abbreviations used in the summaries include: range (R), number of individuals in sample (n), mean ($\bar{x}$), standard deviation (S.D.), coefficient of variation (C.V.), and coefficient of difference between the sexes (C.D.).

DENTITION. The snakes of this species bear teeth on the maxilla, palatine, pterygoid, and dentary. Tooth counts were made on 36 skulls and an additional 432 maxillae on preserved specimens.

The maxillary teeth are long, sharply curved backward, and increase in length and size from anterior to posterior. The posterior two or three teeth are enlarged, heavy, and deeply grooved laterally. These fangs usually are not preceded by a diastema, although a small one may be present in some individuals. Grooves or faint striations on teeth anterior to the fangs are present in about 35% of the maxillae, and may be on as many as 80% of the teeth in the maxillary series. Tooth counts on normal maxillae range from 16 to 27. Taylor (1941) reported a count of 15 for the holotype of Oxybelis potosiensis (=O. aeneus). Dr. Hobart M. Smith (in litt.) has informed me that the maxilla from which this count was made, has probably been lost. One maxilla is still intact on the type, but I did not wish to damage the specimen further by cleaning the tissues from the bone for examination. Two specimens (USC-CRE 742 and 8009) from Costa Rica have counts of 14-19 and 15-18 respectively. The maxillae with the small counts are much shorter than the bones with which they were paired, and although I could find no evidence of breakage, it seems likely that the short maxillae are either incomplete or abnormal. High tooth counts (22 or above) were found in specimens from the Tres Marías Islands, Guerrero in México, Costa Rica, Panama, Colombia, Ecuador, Tobago, the Guianas, the Amazon basin of Brazil, Bolivia, and eastern Perú.

The highest count of 27 is on a specimen from Paramba, Ecuador, that was previously reported by Bogert and Oliver (1945: 385). Low counts of 16 are relatively uncommon and occur in snakes from eastern México, Nicaragua, and Costa Rica. Table 1 summarizes the variation found in the maxillary teeth in various portions of the range. The lowest means for the entire range occur in eastern México north of Ciudad Veracruz, in the Mexican state of Tabasco, and at Bellavista, in northern Perú. Specimens from the mainland of the Mexican west coast average about two teeth more than their east coast relatives. The high counts obtained for the single Guerrero specimen and the Tres Marías sample are conspicuous exceptions for the northern part of the range. From southern Mexico south to Nicaragua, relative uniformity is indicated, but from Nicaragua through Costa Rica, Panama, and in western Colombia and Ecuador, the means indicate a clinal increase of 18.3, 19.5, 21.3, 22.8, and 23.6 from north to south. Unfortunately, the single specimen I have seen from Pacasmayo, Perú, has a mouth that is in poor condition, and I could not determine the number of maxillary teeth present. The mean for specimens from eastern Perú nearly approached that for Ecuador, and means of over 20 were obtained for Tobago, the Guianas, the

Amazon basin of Brazil and Bolivia, as well as eastern Perú.

Summaries of the palatine, pterygoid and dentary teeth are shown in Tables 2, 3 and 4. The palatine teeth number from 9 to 16, the pterygoid from 6 to 14, and the dentary from 18 to 29. As mentioned by Bogert and Oliver (1945: 385), lateral grooves are usually evident on most of the posterior dentary teeth. Faint striae were detected medially on the palatine and pterygoid teeth of several individuals.

CRANIAL OSTEOLOGY. Bogert and Oliver (1945) studied <u>aeneus</u> from various parts of the range and illustrated their discussions with plates of the skulls of specimens from Ecuador and México. They described the prefrontal bones of four snakes from Sonora and Oaxaca, México, Nicaragua and Ecuador and indicated a possible north-south gradient in shape. They noted that the premaxillae of specimens from South America were broader in proportion to the length of the head, with more distinct lateral projections, in contrast to Mexican specimens which had narrow premaxillae with the lateral processes vestigial or absent. These authors further stated that the postorbital bone was reduced in size in the two Mexican snakes they examined. Bogert (1945: 2) figured the premaxillae of specimens of the northern race _O. aeneus auratus_ and the southern race _O. aeneus aeneus_ and noted (p. 12) that the lateral processes were "virtually lacking" in a Mexican example of _auratus_.

I have examined the intact skulls of 36 _aeneus_ from many parts of the range. Skulls of specimens from several critical areas, such as Arizona, Nuevo Leon and San Luis Potosí in México and Bolivia have not been available, and it was not possible in most cases to obtain skulls of similar size for comparative purposes or adequate series of skulls for studies of ontogenetic variation.

Bogert and Oliver (1945) found the prefrontal to be more elongated in proportion to its height in adult Mexican _aeneus_ and less elongated in adult South American specimens. The height/length ratios obtained for this bone in Mexican specimens range from 0.44 to 1.00 and for South American specimens from 0.52 to 0.79. Low values of 0.44 to 0.48 were obtained for adults from Sonora, Sinaloa, and Oaxaca, México. Values higher than 0.52 were common in Mexico, Central America, and South America. The shape of the prefrontal is apparently related to the clinal elongation of the snout that is demonstrated for various parts of the range in the "Size and Proportions" section of this paper. Variation in prefrontal shape is shown in Figure 3.

The postorbital bone does not differ appreciably throughout the range. It is relatively smaller and lighter in young specimens and larger and heavier in older adults. The premaxilla is individually variable in several populations. As can be seen by the examples in Figure 4, the lateral processes are absent or well-developed in specimens from Mexico, Central America, and South America. They are vestigial or absent in three skulls from Sinaloa and Sonora and this modification may be associated with the narrower snout condition or the fact that only three skulls were examined from these areas. In general, bones of the snout differ geographically more than those located adjacent to or posterior to the eye. The nasals, prefrontals, and premaxillae are often proportionally longer and narrower in adults representing populations with longer snouts. Juveniles had relatively short and wide nasals and premaxillae, and shorter prefrontals in all the skulls examined regardless of the population from which they originated.

Variation in the nasal bones is shown by Figure 5. The paired frontal bones lie immediately posterior to the nasals and appear to be little affected by changes in the snout length. The proportions of the bones posterior to the eye change ontogenetically, but few differences were noted that could be related to geographic variation. Two adults from the Pearl Islands of Panama have unusually heavy quadrate and supratemporal bones. Several specimens from other areas have quadrates that are similar, but smaller, and the heavier bones may be due to ontogenetic changes. Very large adults tend to have indistinct sutures and heavy bones, due to an increase in calcium deposition with age.

A detailed account of the cranial osteology of *O. aeneus* is anticipated when additional skeletal material becomes available.

HEMIPENIS. Cope (1900: pl. 28, fig. 16) pictured the hemipenis of *O. aeneus*. Bogert and Oliver (1945) studied hemipenial variation in *aeneus* from selected portions of the range and observed no differences of taxonomic significance. They described the hemipenis of this species (p. 385) as follows:

> The hemipenis is variable in length, extending in the tail from the seventh to the tenth caudals when examined *in situ*. No enlarged basal spines are present. The basal portion is provided with relatively small hooks or recurved, claw-like spines which are staggered in about 10 rows. These spines merge with calyces having denticulated edges after a distance of about two caudals. The calyces are progressively less strongly denticulated toward the distal end. Cope's figure (1900, pl. 28, fig. 16) is approximately accurate except that he indicates small spines rather than hooks on the base. The sulcus is single as depicted by Cope.

I examined the ornamentation on one or both hemipenes of about 60% of the males available for this study. The origins of the paired *retractor penis magnus* muscles were determined for 68 specimens. The description of Bogert and Oliver is applicable to the majority of specimens from most parts of the range. Considerable variation was noted in the number, size, and arrangement of the basal spines, the caudal level at which the spines occurred, the size of the hemipenes, the arrangement of the denticulated calyces, the nature of the apex, and the caudal level at which the *retractor penis magnus* muscles insert.

In situ, the hemipenes normally extend posteriorly to caudal 6, 7 or 8, although in some cases, only to 4 or 5 or as far posteriorly as 9 and 10. The band of recurved basal spines is about two caudals wide and most frequently occurs at the level of the second and third caudals. The nature of the preservative, tension of the retractor muscles, etc. undoubtedly affect the length of the _in situ_ hemipenes and the position at which the basal spines lie. The spines vary in size or are absent. The number of rows ranges from 2 to 12 although their arrangement frequently makes the number an approximate figure rather than an exact one. The _sulcus spermaticus_ is deep and situated laterally on the inverted hemipenis. The sulcus is single, but occasionally forks near the apex. On an everted hemipenis, the sulcus emerges ventrally, but has most of its length on the dorsal surface. The calyces extend from the level of the spines almost to the apex. The calyces vary chiefly in the compactness of their arrangement and the prominence of the denticulated edges. The calyces are reduced distally, but they encroach to varying degrees on the naked apex. Small scattered granular bodies are often found in the flesh of the apex. These may represent reduced denticles. On a fully everted hemipenis, the diameter of the apex is often greater than the diameter of the mid-shaft region. The _M. retractor penis magnus_ inserts at caudal levels from

19 to 27 in Arizona and Mexican specimens, and from 16 to 24 and 18 to 22 in snakes from Central and South America, respectively. The paired muscles usually insert at the same level, but in a few cases, the left or right inserts one caudal in advance of the other.

The nature of the hemipenes necessitates a considerable degree of subjectivity when comparisons are made. Snakes from Zacatecas, Sinaloa, and the Tres Marías Islands differ in having hemipenes much smaller in diameter than those seen on comparable-sized snakes from other areas. In addition, the basal spines are reduced on the Tres Marías specimens, absent in the single Zacatecas specimen, and reduced or absent in the Sinaloa sample. Although occasional adults from other areas have smaller hemipenes than normal, the organs are accompanied by prominent basal spines. Only two of the 25 Sinaloa males examined, have hemipenes that approach the normal size, and both of these have reduced spines. The _M. retractor penis magnus_ of a Tres Marías Island male insert at a level of caudal 20; of the Zacatecas specimen at 21; and of nine Sinaloa males at either 19 or 20. Insertions at this caudal level were found for specimens from Tamaulipas, Chiapas, and Oaxaca and numerous individuals from further south.

Although the hemipenes of the Zacatecas, Sinaloa and Tres Marias Island males are strikingly different from those observed in specimens from the remainder of the range, I have been unable to find other morphological differences which might support specific or subspecific differentiation of any or all of these populations. The hemipenes of the three Tres Marias Island males are in poor condition, but they appear to be similar to those found on Zacatecas and Sinaloa males. The situation seems to be one of sporadic occurrence of similar morphological modifications in three geographically separated populations.

HEAD SCUTELLATION

Temporals. There are usually one anterior and two posterior temporals on each side of the head. The extremes of both are 1 and 4. An increase in temporal number is due to subdivision of the scales themselves or incorporation of portions of subdivided scales in adjacent series. Decrease in posttemporal number occurs when the scales fuse with each other, with the anterior temporal, a parietal, or even a supralabial. One specimen (UCM 30816) has the upper posttemporals fused to the anterior temporals and the lower fused with the last supralabials, and lacks distinct posttemporals on both sides. Enlarged scales posterior to the temporal series are variable in most populations and do not appear to be useful for taxonomic allocation. Table 5 summarizes the variations in the number of temporal scales in the sample studied.

Oculars. These snakes normally possess one preocular and two postoculars on each side of the head. The maximum number of preoculars is 2 and the postoculars vary from 1 to 4. Increase in preocular number is due to the addition of a small scale derived from the dorsal edge of the most anterior labial scale in the orbit. Decrease in postocular number most often occurs by fusion of the two scales, although rarely, one scale fuses with the anterior temporal, supraocular, or supralabial. Increases are frequently due to splitting of the upper postocular or incorporation of a small segment fragmented off the posterior and lateral edge of the supraocular. It is of interest that the holotypes of two synonymized species, Dryophis vittatus Girard and Oxybelis potosiensis Taylor, were described as having unusual ocular counts. Girard (1855) described the holotype of vittatus as having 3 postorbital plates. I have examined this specimen and the "postorbitals" are actually subdivisions of the anterior temporal. Taylor (1941) listed 2 preoculars as one of the diagnostic characters of potosiensis. On the holotype, the extra preoculars on both sides are subdivisions of the supralabials entering the anterior edge of the orbits. I have not seen additional specimens from northeastern Mexico with two preoculars on both sides, although two specimens have two preoculars on one side. Table 6 summarizes geographic variation in ocular number.

Rostral. The length of the rostral scale is greater than its width in the majority of snakes from Arizona and Sonora. The mean width/length ratios drop as the snout decreases in length along the western coast of Mexico. Approximately 90% of the specimens from northeastern and southern Mexico, Central America, and South America have a rostral width/length ratio less than 1.00. Although this character may be of use in differentiating specimens from the northern portions of the range, it appears to be clinal in nature, as is the closely associated longer snout of specimens from the same area. In preserved specimens of aeneus, the rostral scale is distorted more than any other scale, thus few specimens can be measured with any degree of reliability. Very slight distortion during preservation or storage can reverse the length/width ratio. Furthermore, the length must be measured from the anterior tip to the posterior borders which often lie within the mouth cavity. Fleshy folds often obscure the posterior borders of the scale and make mensuration difficult.

Internasals. The internasal scales have been widely used in subspecific determination in this species since Bogert and Oliver (1945) defined northern and southern races based mainly on proportionate differences between the eye diameter and internasal length. The internasal proportions vary ontogenetically and clinally and are closely related to the length of the snout. A detailed discussion of internasal variation and the relationships with the eye, snout and head length is included under the "Size and Proportions" section in this paper.

Prefrontals. The length and width of the prefrontals are affected by ontogenetic and clinal changes, but individual variation is great enough to obscure trends that may be present. Mean prefrontal length/head length ratios tend to increase slightly from Arizona to Panama, but variation is sufficient to negate the demonstration of a clinal increase in the mean values from north to south. Mean values of interest include those for Arizona and Sonora: 0.170; Mexico, except Sonora: 0.172; Central America except Panama: 0.175; Panama: 0.180; Colombia: 0.170; and from 0.170 to 0.180 rather sporadically throughout the remainder of South America.

Frontal. Frontal length ranges from 76 to 98% of the parietal length in most specimens, but occasional individuals have the frontal length equal to or greater than the parietal. The frontal length normally varies between 20 to 30% of the length of the head with the mean percentages for specimens from most areas falling between 22.5 and 24.4%. The frontal may be very narrow or wide enough to reach one or both preoculars. Preocular contact, however, was observed in only about 1% of the individuals studied.

Parietals. Parietal lengths range from 22 to 33% of the head length with the mean percentages for specimens from most areas falling between 25 and 28%. Deviation from the normal condition is due to incorporation of portions of adjacent temporals or postparietals, or fragmentation of the posterior or lateral edges to form additional small scales.

Postparietals. Usually 2 to 4 large scales are in contact with the posterior borders of the parietals. The number, size, and arrangement of these scales varies considerably in individuals from a given area and no particular combination was observed to be limited to a given population.

Nasal. A single nasal scale surrounds each external naris. The scale is elongated and widest medially where the naris is located.

Loreal. Normally, Oxybelis aeneus lacks the loreal scale. Three individuals have additional scales posterior to the nasal. A juvenile from Brazil (MNB R651) has a small scale subdivided off the prefrontal on each side of the head. These scales contact supralabials 2 and 3, the preoculars and prefrontals, but do not reach the nasals. Another juvenile (AMNH 20408) from Ecuador, has sutures dividing the prefrontals into dorsal and lateral scales on both sides of the head. The third individual is from Dutch Guiana (RNHL 13891) and it has the anterior and lateral portion of the right prefrontal divided off as a small scale lying in contact with the posterior border of the nasal.

Labials. Analysis of the supralabial counts of aeneus indicates a degree of regional differentiation. Tables 7 and 8 summarize the more significant aspects of this variation. The regional categories in these tables are those which reflect trends in the populations involved. In Arizona, most of western Mexico, the Tres Marias Islands, the Yucatan peninsula including British Honduras, the El Peten region of Guatemala, Panama, the western coast of South America, Venezuela east of the Andes, Trinidad, and Tobago, the majority of snakes examined have 8-8 or 8-9 supralabials. In Sonora, eastern and southern Mexico, southern Guatemala, Honduras and El Salvador through Costa Rica, northeastern and central Colombia, central and western Venezuela, the Guianas, Brazil, Bolivia, and Peru east of the Andes, supralabial counts of 8-9, 9-9, and 9-10 predominate. Approximately 54% of the snakes from the Guianas, Venezuela, and Trinidad have only 2 labials entering the orbit on both sides of the head, and although this condition is occasionally associated with counts of 9-9 and 9-8, it occurs more frequently with conditions of

8-8 or less. Approximately 2% of the individuals from other parts of the range have only two labials bordering the eye. Additions and reductions in the supralabial counts may take place anterior to, beneath, or posterior to the eye. The lowest supralabial count is 6-6 on MCZ 28042 from Honduras. This specimen has labials 3-4 and 3-4-5 contacting the eye. Fusions anterior to, under, and posterior to the eye are involved in this low count. High counts of 10-10 are found in about 1.6% of the individuals studied.

Approximately 74% of the individuals examined have infralabial counts of 9-8, 8-9, and 9-9, with over 52% possessing the 9-9 condition. Low counts of 6-7 and highs of 9-11 and 10-11 were found in 0.3% and 0.8% of the sample, respectively. Departures from the typical 9-9 condition result from splitting and fusions at almost any point along the infralabial row. Low and high infralabial counts do not necessarily accompany low and high supralabial counts, but there is a tendency for both low supra- and infralabial counts to be associated in Panama, Colombia, Ecuador, the Guianas, Venezuela, and Trinidad. This trend is not evident in most of Central America, Mexico, or Arizona. Infralabials 1 to 4 or 1 to 5 often contact the anterior chin shields regardless of the total count. Occasional anterior fusions reduce the number of scales contacting the anterior chin shields to only three, and in a few cases, one scale, usually number 2, is reduced in size and fails to contact a chin shield. About 0.4% of the snakes examined have one or both of the first lower labials divided more or less transversely, so that the posterior portion appears as an additional anterior chin shield. This anomaly is found in several specimens from Bolivia, but it is a rare condition in other parts of the range. Tables 9 and 10 summarize geographic variation in the infralabials.

Chin Shields. Two pairs of chin shields are normally present in *Oxybelis aeneus*. The posterior chin shields are usually longer than the anterior pair. The means of the ratios of the anterior pair (ACS) to the posterior pair (PCS) tend to increase from north to south, but extreme individual variation and the small sample size from most areas negates the demonstration of clinal increase except on a broad geographic scale. Sexual dimorphism in the comparative lengths of the chin shields is slight. Table 11 summarizes variation in the ACS/PCS ratios. Subadults, or specimens with head lengths (Hl) below 22.0 mm are deleted from the table for greater uniformity of the sample.

Taylor (1941: 128) listed one diagnostic character of the synonymized Oxybelis potosiensis as "the first pair of labials longer than the first chin shields." Bogert and Oliver (1945: 391) noted that Taylor's drawing of the holotype of potosiensis indicated that the 1st pair of labials were actually shorter than the anterior chin shields. I have examined the type (UIMNH 25069) and the chin shields are definitely longer than the first pair of infralabials.

Snakes from Arizona, Mexico, Central America, Colombia, Ecuador, and Eastern Peru normally have the posterior chin shields separated by skin or in contact along their common medial borders. Only occasionally is the area between these borders invested with intergenials. Five specimens from this part of the range have the posterior chin shields completely separated by intergenials, and 29 individuals have three or more small to large scales inserted deeply enough to separate the shields for one-half or more of their common borders. In South America east of the Andes, 118 snakes have the posterior chin shields completely separated by inserted scales. In several examples, as many as 10 or 11 small scales are invested in the membranes between the shields. Only 54 individuals are entirely free of inserted scales. Other South American aeneus possess from one to six inserts and the extent of contact between the shields varies from almost full length contact to separation for about one half of their common borders. The trend toward separation of the chin shields is most pronounced in Bolivia. Twenty-nine specimens from this country have the posterior chin shields completely separated by scales, three have two to five granular scales posteriorly and two have no inserts anterior to the gular scales.

BODY SCUTELLATION

Ventrals. The number of ventrals ranges from 173 (in Ecuador) to 205 (in eastern Brazil). Extremes from Mexico are 175 and 204 and for Central America 174 and 199. The mean ventral numbers for Arizona and Sonora males (193.7 and 194.0) and females (199.0 and 197.2) are the maxima for the entire range. The means are slightly higher for specimens from Nayarit to Oaxaca and the Yucatan peninsula than they are for snakes from Northeastern México, Chiapas, and Tabasco, south to Panama. In South America, relatively low means (below 180) were obtained for females from Ecuador, and males from the Santa Marta Mts. of Colombia eastward across northern Venezuela. High means (above 191) are representative of population samples from Ceara and Pernambuco, Brazil (males), and eastern Perú (females). Means obtained for snakes from the Tres Marías Islands, Bay Islands, Corn Islands, Trinidad, and Tobago, are slightly higher than those obtained from examples of their respective mainland populations. Sexual dimorphism in ventral number is almost negligible. The means are 186.9 for all males examined and 187.7 for the females. Ventral data are summarized in Figure 12.

Anal Plate. The anal plate is normally divided. Only 14 specimens have undivided anal plates, although 18 additional specimens have the two halves partially fused. One individual (AMNH 97074) has the right half of the plate fused with the last ventral. Twenty-one of the snakes with divided anal plates, have the left half overlapping the right, while all others have the right half overlapping the left.

Caudals. Caudal count extremes range from 152 to 197 in Mexico, 158 to 203 in Central America and 137 to 189 in South America. The means range from 167.0 to 191.5 for Arizona and Mexico, 168.8 to 189.6 for Central America, and 154.8 to 179.3 for South America. In general, low means are more frequent for snakes from South America than for those from other parts of the range although the high extremes are frequently above the means for Mexican and Central American samples. Sexual dimorphism in caudal number is slight. The mean is 177.0 for all males examined and 173.1 for all females. Caudal counts were made only on specimens with complete or probably complete tails. Only 55.7% of the specimens available appear to have complete tails. Caudal data are summarized in Figure 13.

Keels. The dorsal scales of *Oxybelis aeneus* may be smooth or weakly keeled. Approximately 47.0% of the specimens from Arizona and Mexico, 49.8% of those from Central America, and 24.4% of the individuals from South America possess keeled scales. Keels were often difficult to detect on old or poorly preserved specimens and the actual percentages of snakes that possess them may be slightly higher than the figures given. They are rarely found near the neck and are almost always more prominent posteriorly than at mid-body. When present, they are usually on rows 5, 6 and 7 posteriorly and 7, 8 and 9 at mid-body, although carination is more extensive on some individuals.

Apical Pits. Apical pits were reported for a Trinidad specimen by Mole (1924: 255). Taylor (1941) noted the absence of these pits on the holotype of *Oxybelis potosiensis*. I examined 20 or more scales from each of 102 specimens, including 13 from Trinidad, and additional scales from numerous other individuals. Apical pits are lacking in every case.

Scale Rows. The dorsal scale rows of *aeneus* are normally 17-17-13. Dorsal scale reduction patterns were determined for 318 specimens including 103 from Arizona and Mexico, 104 from Central America, and 110 from South America. Approximately 70% of the reduction patterns for snakes from each of these areas may be summarized as follows:

Arizona and Mexico:

$$17 \; \frac{\substack{6+7 \text{ or } 7+8 \\ 3+4} \quad (127\text{-}154)}{\substack{3+4 \\ 6+7 \text{ or } 7+8} \quad (127\text{-}154)} \; 13$$

Central America:

$$17 \; \frac{\substack{6+7 \text{ or } 7+8 \\ 3+4} \quad (113\text{-}147)}{\substack{3+4 \\ 6+7 \text{ or } 7+8} \quad (113\text{-}147)} \; 13$$

South America:

$$17\ \frac{\substack{6+7 \text{ or } 7+8 \\ 3+4}\ (107\text{-}147)}{\substack{3+4 \\ 6+7 \text{ or } 7+8}\ (107\text{-}147)}\ 13$$

The mean ventral number for the first reduction drops from north to south. For Arizona and Mexico, the mean ventral number for the first reduction is 135.2, for Central America 134.5, and for South America 132.8. There are two basic variations in the typical formulas above. Either the lateral 3+4 or the paravertebral 7+8 fusion occurs first. This is illustrated by the following examples:

UIMNH 41799 (Panama)

$$17\ \frac{7+8(136)}{7+8(136)}\ 15\ \frac{\qquad}{3+4(144)}\ 14\ \frac{3+4(145)}{\qquad}\ 13 \qquad (187)$$

USNM 120699 (Panama)

$$17\ \frac{3+4(136)}{3+4(136)}\ 15\ \frac{6+7(137)}{6+7(137)}\ 13 \qquad (182)$$

In the latter example, the posterior reduction is paravertebral and essentially in the same row, but the scales are renumbered 6 and 7 rather than 7 and 8, using the recount system proposed by Clark and Inger (1942). Both reductions in most of the <u>aeneus</u> examined occur within

10 scale rows of each other, although the distance separating the mid-body reductions is greater in some individuals. Considering only the snakes with typical reduction patterns, the 7+8 fusion occurs first in 56.8% of the sample from Arizona and Mexico, 58.1% of those from Central America and 61.9% of the individuals from South America. The 3+4 and 7+8 fusions were noted at the level of the same ventral scale in 6.0%, 9.4%, and 8.9% of the Arizona and Mexico, Central America, and South America samples, respectively. In all other specimens the 3+4 fusion occurs first.

Deviations from the formulas above were noted in about 30% of the 317 specimens on which reduction patterns were studied. These deviations may be grouped into five categories.

1. Lateral Reduction Substitution. In this pattern, fusion in scale rows 1 and 2, 2 and 3, or 4 and 5 replaces that which normally occurs in rows 3 and 4. Fusion involving rows 2 and 3 is the most common variation. It was noted on one or both sides of 9 specimens from Mexico, 8 from Central America, and 15 from South America, and is

illustrated by the following example:

AMNH 60764 (British Guiana)

$$17\ \frac{2+3(129)}{2+3(129)}\ 15\ \frac{\qquad\qquad}{6+7(130)}\ 14\ \frac{6+7(132)}{\qquad\qquad}\ 13 \quad (182)$$

2. Vertebral-Paravertebral Combination. Scales in one or both paravertebral rows fuse with a scale in the vertebral row.

AMNH 64248 (Sonora, México)

$$17\ \frac{8+9(137)}{\substack{3+4\\7+8}(137)}\ 14\ \frac{3+4(138)}{\qquad\qquad}\ 13 \quad (199)$$

3. Lateral Substitution for Paravertebral Fusion. Paravertebral reduction replaces a reduction lower on the side.

USNM 110577 (Oaxaca, México)

$$17\ \frac{3+4(127)}{3+4(127)}\ 15\ \frac{5+6(132)}{5+6(132)}\ 13 \quad (184)$$

4. Preanal Increase or Decrease. Departures from the typical 13 scale rows just anterior to the anal were found in 14% of the 1218 snakes studied.

A. Preanal Increase. Increases to 14 or 15 rows were found most often within 6 ventrals of the anal plate. These are due to subdivisions of lateral or vertebral scales.

FMNH 36151 (Yucatan, México)

$$17\ \frac{7+8(142)}{7+8(142)}\ 15\ \frac{\quad}{3+4(143)}\ 14\ \frac{3+4(144)}{\quad}\ 13$$

$$\frac{2=2+3(192)}{2=2+3(192)}\ 15 \qquad (192)$$

B. Preanal Decrease. Decreases to 12 or 11 scale rows are due to fusion of almost any scale on one or both sides of the region just anterior to the vent.

UMMZ 45586 (Colombia)

$$17\ \frac{7+8(106)}{\quad}\ 16\ \frac{\quad}{7+8(111)}\ 15\ \frac{\quad}{3+4(131)}\ 14$$

$$\frac{3+4(135)}{\quad}\ 13\ \frac{\quad}{6+7(183)}\ 12 \qquad (184)$$

5. Sporadic Increase and Decrease. One of the more common pattern deviations is reduction followed by an increase in count, then another reduction,

etc. Such increases are usually limited in extent, but may occur over large areas of the body. In such snakes, unusual counts of 15 to 18 on the neck, 16 to 21 at mid- and posterior body, etc. may be found. It is often difficult to interpret the exact nature of the reductions and increases that occur in these aberrant individuals.

The most conspicuous geographic trends on the dorsal scale patterns are a greater number of 2+3 reductions in South American specimens, and a tendency for the first reduction to occur more anteriorly on snakes from South America than on those from other parts of the range.

SIZE AND PROPORTIONS

All measurements and ratios utilized in this study are ontogenetically variable. For the purpose of this discussion, I have arbitrarily defined the terms juvenile, subadult, adult and large adult in terms of the head length. Juveniles are individuals with head length below 18.0 mm, while subadults are those with head lengths between 18.0 and 21.9 mm. Ratio variations beyond those found in adults are most common in individuals with head lengths below 18.0 mm. Adult snakes are those with head lengths of 22.0 mm or more. Snakes with heads of this length or greater have reached a size that yields comparative stability in the ratios used here. The smallest gravid females examined have head lengths around 22.0 mm, and it is likely that this definition of an adult may be justified in terms of sexual maturity for female aeneus. Large adults are individuals with head lengths exceeding 32.0 mm. Tables 14 and 15 summarize the means of the ratios pertinent to this discussion and include data on the adults only.

Bogert and Oliver (1945) defined two races of O. aeneus on the relative proportions of the eye and internasal scale. The Arizona and Mexican race, O. aeneus auratus, was defined as having the diameter of the eye less than the length of the longest internasal, while the Central American and South American O. aeneus aeneus, had the eye diameter greater than the length of the longest internasal. Bogert and Oliver considered the zone of most abrupt change in proportional eye size to be between Guatemala and southern Oaxaca, and noted that juveniles of the subspecies auratus would not necessarily have low eye to internasal ratios because of the proportionally larger eyes in young individuals as compared to the adults.

Of the specimens I examined, only population samples from the Bay Islands of Honduras, El Salvador, Panama, Colombia, Trinidad, and Bellavista in Perú, have 75% or more of the adults with eye/internasal length ratios (E/IN1) over 1.00. On the other hand, 75% or more of the adults from northeastern and southern Venezuela, the Amazon Basin, Ceara, Pernambuco, and Mato Grosso regions of Brazil, Bolivia, and the Loreto Department of eastern Perú, have the E/IN1 ratios less than 1.00. Snakes with longer snouts generally have longer heads, smaller E/IN1, E/S1 (eye/snout length) and E/H1 (eye/head length) ratios and higher IN1/H1 and S1/H1 ratios. Clinal variation can be demonstrated for several portions of the range by using any of these ratios, but a comparison of the eye diameter directly to the snout length (E/S1) avoids the necessity of compensating for proportional differences posterior to the snout. The means of this ratio clinally increase from Arizona (0.298) through Nayarit (0.339); and from northeastern México (0.328) southward with the exception of the Yucatan Peninsula, to Honduras (0.364) and El Salvador

(0.382). Specimens from Yucatan in México and British Honduras tend to have slightly higher ratio means than those from identical latitudes in southwestern Mexico. Although the means do not appear to be strictly clinal in lower Central America, the highest value for the entire range (0.398) was found for aeneus from Panama. The ratio means decrease clinally from Panama southward along the Pacific coast of Colombia to Ecuador (0.370), and from the Santa Marta Mountains of Colombia eastward to central and eastern Venezuela (0.343). The means increase again from the state of Ceara, southward to the state of Espirito Santo in southeastern Brazil. The mean ratios are relatively high for Trinidad (0.376) and Tobago (0.380). The highest mean obtained for the South American mainland east of the Andes is for the southeastern coast of Brazil (0.384), while the lowest is for the Amazonas region of Venezuela (0.331). Table 14 shows the close geographic correlation that exists between the E/IN and E/S1 means and the actual percentage of adult snakes that have the E/IN ratio equal to 1.00 or more. The absence of close correlation for some populations is ordinarily due to the greater variability of the internasal length as compared to the length of the snout. In view of the tendency of the snout length to change clinally in North and South American populations and the fact that numerous South American snakes have E/IN ratios below 1.00, the subspecies _aeneus_ and _auratus_, as defined by Bogert and Oliver (1945), are not recognized.

The tail length/snout-vent ratio (T/SV) for all _aeneus_ examined ranges from 0.541 to 0.770 and snakes representing the extremes were from Panama. Ratios for juveniles are similar to those obtained for adults. Mean T/SV values are 0.686 for Arizona and Mexico, 0.699 for Central America, and 0.665 for South America. Means exceeding 0.700 were found for specimens from the Tres Marías Islands (0.708), Yucatan (0.716), British Honduras (0.716), northeastern Guatemala (0.705), the Bay Islands (0.715), Costa Rica (0.707), Panama (0.729), and Ecuador (0.708). Means below 0.635 were found for Arizona (0.634), El Salvador (0.629), the Corn Islands (0.618), the state of Amazonas, Venezuela (0.612) and the southeastern coast of Brazil (0.629). Specimens with T/SV ratios of 0.660 or lower occur in the Arizona, Corn Islands, and Amazonas, Venezuela samples. Data supplied by Dr. A. R. Hoge on 24 specimens from the state of Espirito Santo, Brazil, show a mean T/SV value of

0.654. Fewer than 54% of the snakes examined for this study have complete tails. Little or no sexual dimorphism in tail and body proportions is indicated. Clark (1967) reported mean tail length/total length values of 0.388 and 0.374 for eight male and six female aeneus from Nicaragua. The largest specimen examined is a female that measures 1,220 mm from snout to vent. The largest male has a snout-vent measurement of 1,185 mm. Both of these snakes are from the Corn Islands off the eastern coast of Nicaragua. Neither specimen has a complete tail. Bogert and Oliver (1945) noted a possible north-south gradient in mean head width/head length ratios for 28 specimens from both continents. My data do not support such a gradient even when juveniles and subadults are eliminated from consideration. Mean ratios for all adult measurements showing any degree of geographic variation are summarized statistically in Table 15. No measurements or mean ratios other than those affected by snout length appear to have any significance in the taxonomy of this species.

COLOR PATTERN

The color patterns exhibited by _Oxybelis aeneus_ are remarkably variable and difficult to categorize because of gradations in details. Published descriptions of _aeneus_ indicate a considerable degree of color and pattern variability even among individuals from the same geographic region.

Barbour and Amaral (1926: 80) described the holotype of _Oxybelis microphthalmus_ (=_O. aeneus_) from Arizona as:

> Reddish above; throat and upper lip white, the white area on head and neck bounded above by a dark brown line; belly dusky red with a few dark spots and with a white mid-ventral line and a white line on each side along the outer ends of the ventrals; the white ventrolateral lines are conspicuous only along the anterior quarter of the body, the mid-ventral line extends to the vent although it is less conspicuous on the posterior third of the body.

Schmidt and Davis (1941: 266) reported a similar color pattern for an Arizona specimen and noted that the dorsum was mottled with dark spots. Stebbins (1954: 452) depicted different colors for a specimen from the same vicinity as those mentioned above:

> Above ash gray grading into light yellowish brown on anterior fifth or so of body; yellow-brown color deepens

> anteriorly to tan on the head; sides darker gray than dorsum; dark brown stripe on side of head extending from nose through eye to temporal region; sides of jaws cream to pale yellow; ventral color not greatly different from dorsal color--gray, grading through whitish to pale yellow anteriorly; yellow color deepens on underside of head.

Stebbins (1966: 182) provided a brief description similar to his earlier one, but added that the lips were yellow and unmarked and the eye stripe black rather than brown. Wright and Wright (1957: 566) described one living Arizona aeneus as follows:

> The dorsal color of the body proper to the tip of the tail, for about 8 scales transversely is pallid quaker drab, pale mouse gray, or pale ecru-drab. For the first 5 inches the dorsal color is a mixture of buffy brown, sayal brown, or chamois with the pale mouse gray of the dorsal band, and showing little touches of marguerite yellow or seafoam yellow. The top of the head and neck are buffy brown, becoming on the neck almost sayal brown. The scales of the dorsal band are not specked with black or are only occasionally so, while on the sides, under the lens, the first $4\frac{1}{2}$ scale rows are seen to be heavily flecked with black on the dorsal band color, thus appearing to the unaided eye mouse gray or hair brown with flecks of dorsal color.

and another from the same state:

> The middorsal color of the body proper for about 8 scales transversely is drab-gray or smoke gray, with conspicuous interscale color of marguerite yellow or seafoam yellow for 1/3 of its length. In the cephalic half the dorsum is heavily flecked with longitudinal dashes of black. Both the yellow interscale color and the black dashes are particularly prominent in the cephalic 6 inches. The sides of the body are hair brown. The top of the head is drab. There is a clear-cut black line from the eye to the nostril along the upper edge of the upper labials, a prominent black caudal margin to the preoculars. The upper and lower labials are lemon yellow. The iris is black in front and rear with pale drab-gray in the lower portion and above. The pupil rim is pale drab-gray. The underside of the head and neck for 2 inches are pale lemon yellow. From about 3 inches back of the head, the pale lemon yellow of the neck extends as a thin median line down the belly, flanked on either side with cinnamon or pinkish cinnamon. It extends thus for 8 to 10 inches, becoming thereafter a very narrow line of cinnamon or pinkish cinnamon. Very soon, this cinnamon border to the yellow ceases to be a continuous band and becomes a border to the ventrals of mouse gray. The anal plate is cinnamon.

Fowlie (1965: 78) provided a different color description for an Arizona specimen:

> The ground color is a mottled red brown. The throat and upper lip are separated from the brown area by a dark brown line. The belly is reddish with a white line centrally and the ventral scales are white-tipped.

Taylor (1941: 129) described the holotype of Oxybelis potosiensis (=O. aeneus) from San Luis Potosí, México as follows:

> Above and below, on body generally, ashen to brownish gray. The head similarly colored on top and on sides to near labials; labials cream white, separated from the gray color by a black line; chin and throat (and extending a short distance on venter) cream white, the color gradually assuming the ventral coloration. Eye silvery with an anterior and posterior black spot. On anterior part of body transverse black bars, very distinct when skin is somewhat distended. No trace of ventral light lines.

Kennedy (1965: 136) detailed a living specimen from coastal Veracruz, México as follows:

> The dorsum is greyish brown, but there is a gradual transition on the anterior portion of the body towards a light brown or tan which is most pronounced on top of the head. There is a light preocular spot. The canary-yellow of the supralabials just enters the lower margin of the eye and naris but stops abruptly as it meets the tan coloration from the top of the head. The throat is without pattern. The infralabials and anterior chin shields are also canary yellow. This yellow coloration continues onto the anterior ventral scales and gradually fades into a light cream color within the anterior one third of the ventral region. Continuing posteriorly, the greyish brown of the dorsum invades the lateral areas of the ventrals but does not meet in the midline, thereby giving

> the appearance of a small white line about one millimeter in width which seemingly bisects each ventral scale before it is obliterated posteriorly by the dorsal coloration which is continuous in the midline of the terminal part of the body and all of the tail. The undersurface of the tail is almost entirely light brown.

Woodbury and Woodbury (1944: 370) summarized the coloration of nine specimens from Oaxaca, México:

> Ground color generally ashen to brownish gray and brownish red, both below and above. Head above same as body. Supralabials creamy white separated from dorsal head color by a black line which extends from edge of rostral along upper border of labials to neck region. Lower labials, chin and neck are creamy white, the color gradually fading into ground color on first few abdominals.

Del Toro (1960: 170) noted that these snakes have ashy gray or brown ground colors with yellowish-white labials and necks in Chiapas, México. Slevin (1926: 201) mentioned a male from María Madre Island that had a grayish dorsal color with scattered small black spots and a grayish venter. Zweifel (1960: 110) found no differences between aeneus on the Tres Marías Islands and those on the mainland. He described a living snake from María Madre Island as:

> Dorsal color dark brownish gray. The anterior edges of the dorsal scales of the anterior half of the body are yellow,

> but the color shows only when the skin is spread. The ground color of the lateral surfaces is slightly paler than the mid-dorsal region and has spots of the darker dorsal gray. Black marks follow the edges of some lateral scales. Ventral gray with darker spots of brownish gray and a faintly discernible mid-vertebral yellowish gray line.

Schmidt and Andrews (1936: 185) noted dorsal colors of reddish and gray for specimens from Yucatan. Bell (1825: 325) described the preserved holotype of *Dryinus auratus* (=*O. aeneus*) as having shades of pink and light gold over brown, and a metallic lustre.

Color descriptions of Central American *aeneus* have been provided by several authors. Ditmars (1928: 27) reported a gray specimen from Honduras. Slevin (1942: 477) gave this description of a specimen from Boquete, Panama:

> In life the ground color is a light reddish-bronze, with occasional minute black spots; a narrow black line passes through the eye and along the upper edge of the labials; undersurface of body anteriorly greenish-yellow, posteriorly brownish; undersurface of tail brownish.

Taylor (1951: 130) described Costa Rican *aeneus* as:

> Variable in color; green-bronzy, grayish or reddish above, uniform or flecked with brown; a black line on either side

> of the head; yellowish or brownish on venter, speckled or streaked with brown, often with scattered black dots.

Villa (1962: 74) described Nicaraguan aeneus as having light to dark coffee-colored dorsa and white anterior ventral surfaces. Mertens (1952: 69) characterized a living specimen from El Salvador as follows (translated from German):

> Light bronze with scattered sepia spots on the anterior half of the body. Scale margins above and beneath on the body whitish, supralabials yellow-white; on their uppermost margins a black stripe. This stripe divides the lip coloring from the bronze color of the top of the head. Chin and neck yellow-white, with five brick red spots which are present on the supralabials also. The rest of the ventral surface whitish with very fine sprinkling of brown. This powdering densifies on the side of the ventrals in a way that it gives origin on both sides to a fine longitudinal line. On the venter a fine whitish central line may be noted. The iris is a copper-yellow.

Meek (1910: 416) mentioned that these snakes are lighter colored on Margarita Island north of Venezuela than those he had seen from the Venezuelan mainland and Panama. Roze (1964: 224) described Margarita Island specimens as being light gray dorsally and yellowish-white ventrally and sometimes having dark irregular spots on the dorsum. Mole (1924: 255) noted the variability of these snakes on Trinidad and stated:

> In colour these snakes are bronzy, greyish, or reddish brown above, sometimes uniform, whilst others are freckled with brown; usually scattered black dots, or with black edges to some of the scales. There is a black line on each side of the head passing through the eye. The upper lip and lower surface of the head are yellowish white. It is yellowish, pale brownish, or reddish beneath, or it may be speckled or streaked with brown, often with scattered black dots. Sometimes there are two dark brown longitudinal lines. But colour-variation is most difficult to describe.

Johnson (1946: 108) described another Trinidad specimen that was olive-brown dorsally and light yellow ventrally in life. These colors faded to gray and revealed a dorsal mottling in alcohol. Rohl (1942: 316) noted the great variability of coloration in Venezuelan specimens and described the ground colors as yellowish, light brown, or reddish. Roze (1952: 107) categorized a specimen from El Junquito, D. F., Venezuela, as follows (translated from Spanish):

> The head and the center of the dorsal scales are dark brown; the borders are of a lighter brown and therefore well accentuated. Anteriorly, the lighter borders are wider and among these there is something similar to transverse bands, very irregular, that disappear posteriorly. The head, on top, is

> dark brown. All the supralabials are white, as also the infralabials. The two last gulars are brown, the color that continues on the ventrals that are also brown, always with the borders of the scales being lighter. The brown color of the abdomen is lighter anteriorly than posteriorly where it cannot be distinguished from the dorsal coloration. The lighter shade (yellow-brown) of the supralabials and infralabials follows a little over the first dorsals and disappears on the thirteenth ventral, forming two clear stripes on both sides of the head and nape.

Beebe (1946: 36) described a living snake from Kartabo, British Guiana, as:

> Top of head sepia. An indefinite streak along side of head which deepens to a narrow band of black just above the upper labials, and continues across the iris in two areas of dark green. The second to fifth upper labials with narrow shading of black along upper edge. A streak of pale vinaceous buff extends across the top of the preocular, tinging the lower portion of the supraocular and continuing in a horizontal line a little back of the eye, where it deepens to umber. Upper labials pale yellow, shading downward to bluish-white. Throat bluish-white with faint tinge of pink. Body above light ashy, ventral surface dark vinaceous brown. A narrow rim of picric yellow extends around the lower four-fifths of the pupil, widening toward the top and shading to silver white, which extends over all the upper part of the iris. Large irregular patches of parrot green

> lie on either side of pupil flecked with black. The lower part of iris is silvery white flecked with maize yellow.

Wagler (1824: 12) characterized the holotype of *Dryinus aeneus* (=*O. aeneus*) from Brazil as having a brownish dorsum with dark flecks and a golden lustre, a yellow-green venter with scattered dark spots, and a white chin, throat and neck. Wied (1824: 661, 1825: 322) diagnosed the holotype of *Coluber acuminatus* (=*O. aeneus*) as having a dark stripe through the eye, whitish yellow jaw margins and underparts, and a pale gray-brown dorsum with scattered black spots. In his 1825 paper, he noted that *acuminatus* was probably the same species as *aeneus*, but that the former lacked the metallic lustre. Amaral (1925: 24) described two specimens from the Mato Grosso region of Brazil as being grayish and grayish-bronze respectively. One specimen was lightly stained with black, while the other had the borders of the scales slightly greenish and the abdomen covered with black dots. Prado and Hoge (1947: 290) described an adult female from Pucallpa, Perú, as being uniformly gray, spotted with brown and black spots. The specimen had a black lateral stripe through the eye.

Summarization of the pattern variations in aeneus is difficult and subjective. Gradations in every detail occur in most parts of the range. Interpretations of patterns of preserved specimens is complicated by fading, darkening, loss of the more vivid colors prominent in living specimens, and localized discolorations due to preservation and storage methods. Some phases may be common in some areas and rare or absent in others, but most may be found in widely separated populations.

Dorsal scale colors in living specimens include shades of gray, gray-brown, and brown, with numerous specimens having tints of red, orange, yellow, green or black. Both living and preserved specimens may have a metallic or iridescent appearance. Scale interspaces may be white, cream, tan, brown, yellow, orange, red, or black and the color of the interspaces may or may not invade the margins of the scales. Most of the preserved specimens examined are darker laterally than mid-dorsally, although numerous individuals from Arizona through South America are tri-colored with a dark vertebral line, adjacent lighter pigmentation, and dark coloration on the low sides. Some individuals have a peculiar mottling of alternating light and dark pigment, but this pattern also is not limited to any particular geographic region. Occasional specimens are uniformly colored on all or parts of the body. Black or dark brown spots were found on most of the preserved specimens. Bogert and Oliver (1945: 383) commented that the black dots often found on the skin of Mexican aeneus seemed to vary only within narrow limits, but their conclusions were based on relatively few specimens. In specimens examined from Mexico and other parts of the range, these black dots are abundant, moderately abundant, sparse, or absent; limited to certain body regions or present over most of the dorsum and venter; variable in size from small stipples to irregular flecks or spots as large as 4 mm in diameter. They may be regularly distributed as paired lateral spots on some or most of the ventrals or even fused into lines or a reticulate pattern on the back, sides, or belly. Most aeneus have black or dark brown patches arranged in diagonal or vertical rows for about 2/3 of the body length. These patches form a "checkerboard" pattern in many individuals. The pattern is conspicuous or visible only when the skin is stretched. The dark pigment patches occur most frequently on portions of two scales and the interspaces between them, although in numerous individuals they occupy the greater portions of 6 to 8 scales and the adjacent interspaces. The patches are usually largest anteriorly. In occasional snakes, the checks are visible from the neck almost to the anal plate, while in others they are present only at mid-body, visible only as weak traces on a few scale interspaces, or absent. In living snakes, the dark patches may be bordered by areas of red, orange or yellow pigment, but the borders are discolored or absent in preserved specimens. I have seen living specimens from Mexico and Colombia that lacked the black or brown pigments entirely, but had yellow, orange or red interspaces alternating with unpigmented interspaces.

The dorsal and lateral surfaces of the head and neck are usually colored similarly to the body, but a shade darker. A light area is present on the superior portions of the oculars and occasionally on adjacent scales. A dark brown or black stripe normally begins at or near the posterior edge of the nasal, runs posteriorly along the upper edges of the supralabials and lower edges of the adjacent head scales, then terminates at a point varying between the last supralabial and 18 scale rows onto the neck. The stripe is wide or narrow, restricted to only a few scales or absent. It is frequently accompanied by a mask of dark brown or black pigment on the sides of the temporal region and snout. When present, the mask is inconspicuous or prominent and represented by fine stippling or dense areas of pigment.

Coloration on the ventral surface varies considerably within a given population. At mid-body and posteriorly, preserved snakes most frequently have colors similar to that of the dorsum, but a shade lighter or darker. The darker colors present posteriorly usually become lighter anteriorly as they grade into the yellows, cream or white of the neck region. In numerous specimens, however, the darker colors are lighter anteriorly, but extend as shades of gray or brown onto the most anterior ventrals and rarely onto the chin shields. These extensions of the darker ventral pigments occur laterally, centrally, or uniformly on the anterior ventrals. Some individuals from Venezuela and the Guianas have the light colors of the neck extending for the full body length, but others have darkly pigmented venters and intermediate examples are evident in the sample. In specimens with dark ventrals, the posterior edges of these scales are light in color. A thin longitudinal medial light stripe and paired lateral dark brown or black stripes are usually present on the ventrals. These stripes may be conspicuous or inconspicuous, continuous or interrupted, restricted to certain portions of the venter or absent. A few specimens have white, cream or yellow stripes formed by an absence of pigment on the lateral edges of the ventrals and the lower portions of the scales in the first dorsal row. Such stripes are rarely conspicuous and are usually limited to the anterior and mid-body regions. Most aeneus have numerous white flecks on the mid-body and posterior ventral scales. These flecks may be scattered over the scales, but they tend to be larger and more concentrated at the lateral corners of the scales. They are absent in some specimens.

The coloration of the tail is mostly identical to that of the posterior body regions, although the tip tends to be darker or more frequently tinted with shades of blue or green.

The labials and ventral head scales of preserved snakes are normally white, cream, or yellow, but occasionally have spots, patches, fine mottling, or relatively uniform areas of brown, red or black pigment. Individuals with red or reddish-orange pigment patches on the labials, chin shields and anterior throat regions are common in the Corn Island sample, but this condition was found in occasional individuals in widely separated populations on the Central American mainland and Colombia. With the exception of discolored specimens on which the throat condition in life could not be determined, and the red-throated individuals just mentioned, the labials and chin shields of snakes from Arizona and México to Panama rarely have spotting or mottling of any sort. In South America, pigmentation on the labials and chin shields takes a variety of forms and occurs on numerous individuals. All but two of the specimens from Bolivia have a fine powdering of brown or black pigment on the gulars, intergenials and chin shields. The pigment is dense and widespread in some snakes and limited to the scale centers or edges in others. It is accompanied by small black spots in some individuals. Similar fine powdering is found on the throats and chins of a few specimens from Brazil and Venezuela, and on the preventrals and anterior ventrals of specimens from Central America and Mexico. Two of the Bolivian specimens have chins that lacked traces of pigmentation. The dark spots are also found on snakes from Colombia and the Guianas. When this spotting is prominent and restricted to the central portions of the labials and chin shields, the resulting pattern is similar to the condition in Oxybelis argenteus. All specimens from the Río Ucayali drainage in the Loreto Department of Perú have some degree of dense black or brown mottling on the chins and throats. The extent of the mottling ranges from covering almost the entire top of the head, chin and throat to being restricted to portions of the chin shields, intergenials, and gulars. The degree to which this mottling has been produced or affected by preservatives is not known. John P. O'Neill supplied me with a 35 mm Kodachrome slide showing the body and side of the head of a live aeneus from the region 15 km northwest of Pucallpa, Perú. Although it is difficult to judge from the slide, the dorsum of the head does not appear to have the mottling and the labials are immaculate cream or white. The chin and throat appear to be dark medially, but the nature of the pigmentation (or shadow?) cannot be discerned. The color description of a Pucallpa specimen given by Prado and Hoge (1947: 290) mentions nothing concerning the coloration of the chin and throat. In view of the pronounced color changes evident in so many preserved aeneus, I do not feel it wise to assign subspecific status to this population at this time.

Albinism and melanism have not been reported for this species. Several cream-colored or very light gray specimens were examined, but all have normal colored eyes and have been preserved for many years. Several specimens are black over the entire body, head and throat, while others have obvious localized areas of black discoloration. Correspondence and conversations with the collectors of several of these black specimens revealed that the snakes were normally colored in life. Numerous preserved specimens are discolored to the point of being a rich dark brown. Specimens that are light gray or tan with white or yellow throats in life, may be dark brown dorsally and have dark brown throats in preservatives. Discolorations of these types are frequent in the sample studied.

Ontogenetic changes or sexual dimorphism in coloration is not evident in the preserved specimens examined. Bogert and Oliver (1945) studied 96 specimens of aeneus from various parts of the range and stated (p. 383): "With reference to pattern differences we have been unable to observe any constant differences that might serve to differentiate populations." With the exception of the Peruvian snakes with mottled throats, my observations tend to support these conclusions.

NATURAL HISTORY

FOOD. The diet of *Oxybelis aeneus* consists of small lizards, frogs, birds, and insects. Little is known concerning the feeding habits under natural conditions. A summary of the animals utilized as food under natural conditions appears in Table 16. Although these snakes are primarily arboreal, certain of the species preyed on in nature indicate that at least some feeding takes place at ground level. Mertens (1952) has mentioned an *aeneus* in captivity fed on juvenile *Ctenosaura completa*. Of the snakes I examined for this study, thirty-two with obvious body bulges were inspected through small incisions in the gut to determine the nature of the food present. Thirty contained lizards, one a leptodactylid frog, and one had remains of roaches. One Mexican specimen I maintained in captivity for 16 months, accepted the lizards *Anolis carolinensis*, *Eumeces fasciatus*, and *Sceloporus undulatus* on numerous occasions, but with a single exception, refused roaches, crickets, grasshoppers, hylid frogs, small birds, and juvenile mice and hamsters. On one occasion, this snake caught an adult *Hyla versicolor*, quickly worked its fangs into the frog's back, and then for no apparent reason, released the animal unharmed except for a few skin punctures. The frog was still alive and active on the following day. A captive specimen from Colombia fed readily on various lizards and hylid frogs. I have been told of a Florida animal dealer who feeds roaches and crickets to captive aeneus, but I was unable to verify this.

Little is known about the number of prey animals this vine snake consumes at a single feeding. Beebe (1946) noted one specimen that contained two small tree frogs and another that had ingested a single tree frog (Hyla rubra) and a bird (manakin). Smith and Grant (1958) mentioned a specimen from Panama that had eaten two lizards (Gymnophthalmus speciosus). On one occasion, the Colombian snake I observed, ate seven subadult and adult anoles (Anolis carolinensis) in less than one hour. Netting (1936) reported an aeneus measuring 847 mm in body length, that had swallowed a basilisk lizard (Basiliscus basiliscus) measuring 275 mm in length from the forelimbs (the head was digested). Apparently this is the largest animal yet recorded in the diet of the species.

Feeding behavior has been described by Fischer (1882), Mole (1924), Vorhies (1926), Schmidt and Davis (1941), Ditmars (1937), Stebbins (1954, 1966), Wright and Wright (1957), and Fowlie (1965).

Greenhall (1936) noted that snakes of the genus *Oxybelis* drink from rain and dew collected on leaves. He provided water for captive specimens by shaking droplets from a broom onto vegetation in the cages. Mertens (1952) observed *aeneus* drinking small water droplets on vegetation in a cage. I have never observed a captive specimen in the process of drinking.

VENOM AND BITE. No less than seventeen authors have termed these opisthoglyphous snakes as deadly poisonous to their prey, but only mildly poisonous to man. Brief descriptions of the effects of their venom on small animals have been published by Vorhies (1926), Ditmars (1928, 1931, 1937), Schmidt and Davis (1941), Rohl (1942, 1956), Cochran (1943), Stebbins (1954, 1966), Del Toro (1960), Villa (1962), and Fowlie (1965). Dunn (1944b) commented on the serious effects of the bite of this species, but added that the bite was not necessarily fatal to humans. He further stated that this snake caused the major proportion of snake-bite accidents in Colombia. Crimmins (1937) described a bite on the middle phalanx of the right forefinger of a human. The snake held its grip for 10 to 20 seconds and had to be pried loose. Itching, redness, slight swelling, numbness, and a large blister occurred in the region of the bite within the first 10 minutes. Fowlie (1965) reported localized blistering and numbness which subsided after a short time in another bite involving a human victim. On 18 January 1965, Larry D. Wilson of the Louisiana State University Museum of Zoology voluntarily submitted to a bite by an adult aeneus from México. Wilson was bitten on the right thumb and the snake was allowed to maintain its grip for approximately 30 seconds after the rear fangs appeared to be inserted into the flesh. Other than a very slight and temporary reddening of the skin around the punctures, Wilson evidenced no reaction. On another occasion, I was bitten on the knuckle of the right thumb by a Colombian specimen attempting to escape from its cage. The only reaction was a localized red inflammation of about 6 hours duration.

REPRODUCTION. Stebbins (1954: 454) noted that a female aeneus from Arizona had four oviducal eggs, the largest about 62 mm long, but he failed to mention the date on which the snake was killed. Campbell (1934: 9) discussed an

Arizona specimen taken on 24 July 1933 that had four eggs in the oviduct, the largest measuring 5.5 cm in length. Neill (1962: 243) reported an adult taken in British Honduras in April that "did not contain large eggs." Rand (1957: 530) described a female from Los Blancos, El Salvador, that contained five well-developed eggs when it was captured, although two dates (21 March and 21 May 1951) were mentioned as the date of collection. Sexton, Heatwole, and Knight (1964: 271) reported four eggs of this species on a hillside in undisturbed, mature, open forest in Darién Province, Panama. Sexton and Heatwole (1965: 40) described the same clutch in the following detail:

> "A clutch of 4 eggs was found in a depression in the leaf litter at the upper side of a large tree on a sloping hillside on July 1, 1961. The area was one mile upstream from the mouth of the Canclon River. The dimensions of the eggs were: 37 X 14.8 mm, 35.8 X 15.2 mm, 34.1 X 15.2 mm, 37.9 X 14.6 mm. The eggs were white with irregular brown stains and adhered to each other. One was opened and found to contain a well-developed embryo with a total length of 22.1 cm. The remaining 3 eggs hatched on July 13, 1961. Two of the hatchlings were measured. Both were 37.4 cm in total length (22.6 and 22.9 cm snout to vent)."

Cochran (1946: 7) noted a female from the Pearl Islands of Panama that contained four cylindrical eggs nearly ready to lay, when captured on 18 July 1944. Beebe (1946: 36) said that a six-foot female captured in Venezuela on 17 March 1924 contained three "fully-formed eggs measuring 7 by 17 mm." Mole (1924: 256) observed a Trinidad specimen that laid 6 large eggs in June.

Fully formed eggs were found in three aeneus having snout-vent lengths as small as 590 mm. The head lengths of these three snakes vary from 21.8 to 22.1 mm. As only snakes with obvious body bulges were examined internally, the species may reach sexual maturity at even smaller sizes.

PARASITES AND PREDATORS. Beebe (1946: 36) wrote: "A five-foot snake captured on February 24, 1922, had three large ticks fastened to the head, one of which, on the left lower side of the jaw, had worked half-way back from the tip of the mandible, inducing such severe injuries that the entire jaw was shrunken and distorted." Seventeen of the specimens examined by me had ticks fastened to some part of the head or neck. Several of the snakes had two or more ticks, and one had 26 attached around the head or neck. In a few specimens, ticks were fastened to the tissues inside the orbit.

Wright and Wright (1957) reported a conversation with a Mr. Kimmel who stated that snakes of this species were rare in southern Arizona, because they were eaten by javelinas. Beebe (1946: 36) observed an aeneus in tall bamboo that "was so mobbed by small birds and jays that it fell thirty feet to the ground close by me."

LOCOMOTION. Wagler (1824), Ruthven (1922), Ditmars (1928), Beebe (1946) and Fowlie (1965) have described arboreal locomotion in snakes of this species. Stejneger (1901) and Stebbins (1954) briefly described their movements on the ground. Schmidt and Inger (1957: 231) termed the vine snakes of the genus Oxybelis "extremely slender and slow-moving forms." Ruthven (1922: Plate X) referred to Oxybelis acuminatus (=O. aeneus) and stated "An arboreal species which has such a slender body that it can move directly through the branches of trees at an astonishing speed." Beebe (1946: 36) commented on the same species: "When disturbed they vanish almost between winks, and the instantaneous dash twenty or thirty feet away leaves the eye completely baffled." Zweifel and Norris (1955) have noted rapid locomotion on the ground in this species. Fowlie (1965) stated that these snakes have been observed to jump readily from one tree or bush to another.

MISCELLANEOUS BEHAVIOR. Mole (1924), Wright and Wright (1957), and Kennedy (1965) have reported a curious, fairly rapid and rhythmic, vibration of the anterior portion of the body in these snakes. I have observed this phenomenon in several living specimens. Apparently, these movements can occur whenever the head and anterior portions of the body are rigidly extended and free of support, whether the snakes are crawling on the ground with the anterior portion of the body elevated, reaching from one branch to another, or slowly approaching prey. Mole (1924), Ditmars (1928), Oliver (1955), and Stebbins (1954) have described a motion of gentle, lateral swaying in these snakes which supposedly imitates the movements of a twig in a light breeze. Mole has noted that this swaying may occur in caged animals when no breeze is present.

Snakes of this species often protrude their tongues and hold them motionless for varying periods of time. Literature accounts of this have appeared in Mole (1924), Beebe (1946), Del Toro (1960) and Kennedy (1965). Procter

(1924), Curran and Kauffeld (1937), and Hediger (1955) have mentioned tongue protrusion in the genus *Oxybelis* as a mechanism for fascinating prey. My observations on captive *aeneus* do not seem to confirm this. These snakes approach prey by rapid pursuit or by slow, almost imperceptible movements. In the case of rapid pursuit, the specimens observed by me never protruded their tongues. In the slow approach, the snakes moved to within two to six inches of their prey, then made quick, lunging bites. Tongue extension may occur frequently, rarely, or not at all during the slow stalk. I observed one vine snake stalking anoles 112 times during a three-month period. The animals being stalked were obviously aware of the snake's approach only 37 times. Of the 37 cases of prey awareness, the lizards made 12 escape attempts and only in nine instances did the anoles watch the approaching snake with any sort of gaze that indicated "fascination." Even in these nine cases, the snake's head and not its tongue seemed to be the focal point of the lizard's attention. Furthermore, the frequency of the snake's tongue protrusion was not noticeably different when the anoles were looking in the direction of the stalking snake. In view of the ordinary responsiveness shown by frogs and lizards to moving objects, it seems likely that an organ intended to attract their attention would have to exhibit some sort of movement. I suggest that the immobility of the tongue of these snakes is an adaptive mechanism to maintain olfactory contact with the environment without attracting undue attention. The longer duration of tongue protrusion might therefore be necessitated by the time needed to concentrate scent particles on the tongue tips to the threshold level required for adequate detection by Jacobson's organs. This adaptation would seem to fit in well with the numerous body features and behavioral patterns of this species that contribute to the ability of these snakes to blend harmoniously into the habitat and thus escape detection.

TAXONOMY

No subspecies are recognized.

Oxybelis aeneus (Wagler)

Dryinus aeneus Wagler, 1824: 12
Oxybelis aeneus, Wagler, 1839: 183

HOLOTYPE. ZSM 2645/0, a female from the forests adjacent to the Solimõens River, near Ega, Brazil. According to Bogert and Oliver (1945: 389), Ega is an older name for the town now known as Teffé near the center of the state of Amazonas.

DEFINITION. A long-snouted, arboreal species in the genus *Oxybelis*. This species may be distinguished from others in the genus by combinations of the following characters: Dorsum basically grayish or brownish and lacking stripes; venter gray, tan, or brown posteriorly; ventral stripes relatively indistinct or absent; eye diameter/snout length 0.254 to 0.505 in adults; snout length/head length 0.319 to 0.480 in adults; supralabials 7 to 10, rarely 6, with two or three scales entering the orbit; infralabials usually 7 to 10, rarely 6 or 11; anal plate divided; dorsal scales

17-17-13, keels weak or absent; maxillary teeth 16 to 27; palatine teeth 9 to 16; pterygoid teeth 6 to 14; dentary teeth 18 to 29; hemipenis undivided.

DESCRIPTION OF HOLOTYPE. Wagler (1824) furnished a detailed description of the holotype. The following account supplements the one he provided. Scutellation: oculars 1+2, temporals 1+2, loreal absent, supralabials 9, infralabials 9, chin shields 2, intergenials 2, ventrals 197, caudals 172. Body length is 730 mm, tail length 309 mm, head length 24.4 mm, snout length 10.1 mm, eye diameter 3.6 mm. Dorsal scale reduction formula is:

$$17 \frac{3+4(147)}{3+4(147)} 15 \frac{6+7(155)}{6+7(155)} 13 \quad (197)$$

Wagler noted 203 ventrals and 180 caudals for this specimen. His counts were apparently in error.

Wagler described this specimen as being golden-brown or bronze with a metallic lustre dorsally and brownish ventrally. The snake has lost most of the original scales in preservatives and the dorsum is now gray. Black checks are prominent on the many scales and the interspaces. These become indistinct a short distance posterior to the mid-body region. A black eye stripe extends about 8 scale rows onto the neck. The labials and chin shields are white. The venter is light brown with numerous scattered flecks of white. The midventral light line is almost absent and no lateral stripes are evident.

LIST OF SPECIMENS EXAMINED

ARIZONA: ASDM 1828, 2276; ASU 6735; CM 29379; CU 2655, 4072; MCZ 22417; UA 16786; UCMVZ 52240; UMMZ 75779. BAY ISLANDS: BMNH 95.1.17.2-10, 95.2.20.20; CM 27609, 27615; FMNH 34544-34546, 34564-34581, 53834-5; TCWC 21916-8; UK 101451. BOLIVIA: AMNH 30879, 35984; CM 2766-7; 2825, 2827, 5085; FMNH 35705-10, 140195; MNB 11908; TU 18069; UMMZ 60785, 60786(2), 60787, 63197, 63198(3), 63200(3), 67988)3), 67989-67992, 67993(2), 67994. BRAZIL: AMNH 3886, 59385, 87955; ANSP 5260, CAS 49345, 49793; FMNH 19203, 49792; IRSNB I.G. 9.615, Reg. 589β(2), I.G. 22.279, Reg. 9.834-5(2); MCZ 2582, 2778, 53207-12; MNB R373-4, R650-7, R1547-8, R1930, R1945-6, R1962, R2498; MNHN 3650; SNM 20272-3; UMMZ 65848, 109012; USNM 6003, 100744; ZMN 2376, 2381, 30311; ZSM 2137/0, 2645/0(Holotype). BRITISH GUIANA: AMNH 8170, 8180, 14260, 18179, 18180, 36046, 36115-6, 60758-66, 60770-6, 60812, 60815, 60839, 60853; UMMZ 47764, 56462, 65163(2), 80427, 85275; UM 55-142; USNM 145459. BRITISH HONDURAS: CUM 25875; FMNH 4209-11, 4443, 5632, 6972, 49353; MCZ 66359, 66360, 71652; UMMZ 80711-12; USNM 55905; ZSM 677/20.

CENTRAL AMERICA (No other data): USNM 16414; IRSNB I.G. 9.422, Reg. 401δ; ZSM 899/20(2). COLOMBIA: AMNH 17608, 35254, 35512-3, 91815; ANSP 25637-8, 25746-7; CM 171-5, 184, 2010; FMNH 27577, 28324, 30788, 43739-40; IRSNB I.G. 4.544, Reg. 401ξ; LACM 2644; MCZ 1987, 2697, 32731; MNHN 3619; RNHL 7846(2); SM 1852(4); UCMVZ 71540; UMMZ 45584-90, 54947, 76026; USNM 4306, 144176; ZSM 124/37. CORN ISLANDS: AMNH 97074-92; UK 86215-8, 101452-3. COSTA RICA: AMNH 17346-8, 17350, 17352, 6443, 69715, 89169; ANSP 19516, 22265, 22366; BMNH 95.1.4.11, 1933.6.22.10; LSUMZ 14133; MCZ 56085-9; TCWC 21786; UAHC 61-230; UCR 510, 512, 513, 612; UF 4017, 10219, 10280; UK 31894, 35746-8, 86585; USC(-CRE): 30, 90, 121, 539, 633, 709(3), 742, 2908, 2909(2), 2998, 6247, 7100 7103, 8009(2), 8242(2), 8254, 8262, 8283; USNM 32576-7, 37759, 148020-2; ZMN 2382(2). DUTCH GUIANA: IRSNB I.G. 4.254, Reg. 401γ(4); RNHL 794, 811(3), 821, 7680(2), 7682(2), 7683, 13885-99; SM 84(2); ZMN 2379, 2380, 7398. ECUADOR: AMNH 13437-8, 13440, 13585-8, 20408-9; CM 9925, 22551; FMNH 4058; JAP 3699; UMMZ 83713; USNM 12350; ZMN 16456. EL SALVADOR: FMNH 10997-8; SNM 42034, 42498, 45405, 51943; UK 62112; USNM 4951. FRENCH GUIANA: MNHN 3651(2). GUATEMALA: AMNH

38078; ANSP 19606; BMNH 64.1.26.123; FMNH 191, 20088, 20170, 20418, 43380; IRSNB I.G. 2.611, Reg. 401; LSUMZ 9674; MNHN 6088; NMB 2085; RNHL 814; SM 2438; SU 4080; TNHC 29665; UCMVZ 24614, 30816-9; UK 55720, 58098-9; UMMZ 74908, 91027, 98284-7, 106730, 107277-82, 117953(3), 118258; USNM 35914, 38434, 64907. HONDURAS: AMNH 46990, ANSP 26658; FMNH 5300, 27050, 34470, 40872; MCZ 19948-9, 28042, 38766, 49851-5, 49930, 49936; NMB 9027-8; SDSNH 3571; TCWC 21915; UMMZ 58409, 58414, 63356; USNM 17809, 20265-6, 82164. MEXICO: AMNH 3881, 3887, 3888, 4308-9, 19830-6, 38841, 60456-7, 61050, 63739, 63740, 64247-8, 64597-8, 64744-5, 65941, 66457, 66799-66801, 67977-84, 68550, 71657, 75612, 75953, 87605, 89622, 97977-8; ANSP 18261, ASDM 1751; ASU 6688-9; BCB 11146; BMNH 82.11.15.45-8, 90.10.10.81-84, 95.1.17.1; CM 7251; CUM 12967; FMNH 20615, 34652, 36139-65, 38435-73, 40744-5; IHN 176, 272, 544; IRSNB I.G. 536, Reg. 401β(2), I.G. 9.422, Reg. 401ε; LACM 2643, 7011-20, 7235-6, 10087; LSUMZ 6918; MAZG 347; MCZ 7870, 26827-8, 27803-5, 33669-78, 43277, 45555, 46405, 46792-3, 55821; MNHN 6108; MSU 1880, 4175H; NMB 6423; SDSNH 7385, 18189, 19684, 44054, 44055; TCWC 7313, 7460-3, 9158, 9516-7, 11584, 11637, 21388, 21543, 21908; TU 18071;

UA 16789, 16791, 16795, 16797-9; UCMVZ 26161, 45170-8, 50815-28, 51642, 57260, 59297-8, 71357; UIMNH 6205-9, 11275-85, 18694-700, 25069, 34920, 34998, 37268, 37303, 39156-7, 41052, 41436, 41575, 42855, 46912, 47870, 47895, 48810-12, 52978, 57173; UK 23795-6, 27190, 27574-6, 29497, 37593, 39629, 39643, 39965, 58097, 68935, 70878, 73584-600, 77978, 80759, 83409, 87463, 100511, 102969-70; UMMZ 73084, 80211, 82654-65,84258, 85685-96, 87665-71, 88254(2), 88300, 88312, 94590, 10405-8, 104677-81, 108788, 110823, 110943, 112511, 114605, 115577, 117696, 118445, 118942, 122038, 122831; USL 6021; USNM 5318, 6627(2), 16394, 25205, 30177, 30482-3, 32347, 46455, 46461, 46501, 46565, 46606, 67375, 105306, 110565-84, 122059, 123495; ZMN 2378. NICARAGUA: AMNH 12693-6, 17349, 75222; ANSP 5257; BMNH 94.7.26.43; LACM 10089-90; MCZ 3816, 9572; TCWC 19245; UK 42324, 86219-30; USNM 5576, 15640, 16392, 20684, 25238, 148528. PANAMA: AMNH 67059, 90055-62; ANSP 5256, 5258, 22563, 22970; BMNH 1926.1.20.81-2; CAS 71432-3, 98261, 98426-7; CM 6863, 7660, 7670, 7695, 7697; FMNH 2636, 6119, 13348, 16732-5, 83552, 161478; LACM 10088; MCZ 2704, 2713, 4808, 9897-8, 9919-23, 9949-57, 16389-90, 18835-6, 22220, 22231, 22236, 22259-61, 22274, 23880-84, 25092-4, 25118, 26627-8, 28062, 31551, 34285, 37059-60, 37101, 39777, 42747, 42785, 43938; MNHN 85-158; NMB 7646-50; SDSNH 16594, 25278; SU 13724; TNHC 23955; UIMNH 41774-41804, 42130-1, 52751; UK 61084-7, 75730, 80231-6; UM 55-140; UMMZ 57926, 63698-700; 83520, 90329-30, 95491-3, 124134-5, 124171, 124187; UNM 6836; USNM 7315, 50108, 50122, 65869, 82175, 120657-75, 120699, 129928, 140061, 140703-4, 148248, 148264; ZMB 2377. PERU: AMNH 52193, 52511, 53109, 53794, 54251, 54353, 55084, 55528, 55991; FMNH 40085, 45569; MCZ 17417-9; NMB 5653; SNM 20271. SOUTH AMERICA (No other data): ANSP 5254-5; NMB 2084. TOBAGO: BMNH 1931.10.18.144; MCZ 11996; NMB 12730, 19291. TRINIDAD: AMNH 8351, 8363, 64471, 73129-33, 85943-4; BMNH 1931.10. 18.138, 1940.3.11.86; FMNH 49973-85; MCZ 6116-7, 80997; NMB 7768, 8996-7; UF 3627, 16490; UMMZ 123048; USNM 12374(2), 17747. VENEZUELA: AMNH 59404, 59431, 61034, 61038, 77120; ANSP 18289-90; CM 7281, 7286, 7344, 17395; FMNH 2589, 2675, 4057, 17839-40; MCNC 7, 382, 391, 480, 517, 559, 583, 617-8, 663, 718, 930, 1007, 1401, 2018, 2033, 2046, 2233, 2257, 2263, 3008, 3013, 3031, 3060, 3068; MCZ 9991-2, 43583; NMB 2086, 9579, 13567, 13820; RNHL 7852, 7853; USNM 22536, 27825, 12120; ZMB 2383-4. NO LOCALITY DATA:

AMNH 73052, 73092; UIMNH 18697.

SPECIMENS NOT EXAMINED

Dr. A. R. Hoge supplied scutellation data and locality information on the following specimens in the collection of the Instituto Butantan:

BRAZIL: IB 385-6, 491, 971, 1058, 1284, 3129, 3185, 8174, 8190, 8463, 8511, 8563, 8571, 8661, 8743, 8762, 8789, 8861, 8863, 8940, 9110, 9117-8, 9413, 9421, 9443, 9731, 9776, 9857, 12025, 12539, 13008, 14215, 14655, 14659, 14660, 14669-70, 14701-2, 17580, 17833-4, 20143, 20185, 20214, 20675, 21086, 22921, 23570, 24004-7, 24582, 24916-7, 25327, 25493, 25937, 26534, 26650. TRINIDAD: 1202, 1259, 1280. VENEZUELA: 19427-8, 25736-9.

SUMMARY AND CONCLUSIONS

The nomenclatural history of Oxybelis aeneus is reviewed. The name Dryinus aeneus Wagler, 1824, is given preference over Coluber acuminatus Wied, 1824, primarily on the basis of a reference to the "Serpentum Brasiliensium" in a March, 1824, publication of Spix and Martius. All synonymized forms of aeneus are discussed and the present locations of the holotypes are given. The holotype of Dryinus auratus Bell is considered lost.

Bogert and Oliver's (1945) concept of two subspecies, O. aeneus aeneus and O. aeneus auratus, based on the relative proportions of the eye diameter and internasal scale length (E/IN1) is examined. These authors were correct in noting that the most abrupt change in mean E/IN1 ratios of North American aeneus occurred somewhere between Oaxaca (Mexico), and Guatemala. North-south clines for the mean E/IN1 and eye/snout length (E/S1) are demonstrated for Arizona through Nayarit and for northeastern México to Honduras and El Salvador. The mean E/IN1 ratios are near 1.00 in Chiapas, Tabasco, and Yucatan, México, and it is in these areas that the percentage of adults with ratios over 1.00 sharply increases to 50% or more. This is the situation that would be expected as the two measurements involved become nearly equal. Clinal changes in these ratios are demonstrated also for Panama southward to Ecuador, western Colombia to eastern Venezuela, and from Ceara south along the eastern coast of Brazil. The only population samples that have 75% or more of the adults with E/IN1 means of 1.00 or more, are from the Bay Islands, El Salvador, Panama, Colombia, Trinidad, and Perú (Bellavista). Conversely, 75% or more of the adults from northeastern and southern Venezuela, the Amazon Basin, Ceara-Pernambuco, and Mato Grosso regions of Brazil, Bolivia, and the Rio Ucayali drainage of Perú (all within the range of the race aeneus) have the E/IN means below 1.00. On the basis of these data, the subspecies, aeneus and auratus, as defined by Bogert and Oliver (1945), are not recognized.

No geographic differences in head scutellation other than those associated with the length of the snout were noted. The rostral tends to be longer than wide in Arizona and Sonora, and about as wide as long elsewhere in the range. Occasional individuals from other areas have long rostral scales, however. Supralabial counts center around 8-8 in some areas and 9-9 in others. A large number of individuals from Venezuela, Trinidad, and the Guianas have only 2 supralabials bordering the eye, but a few specimens from other areas duplicate this condition. The mean chin shield ratios (ACS/PCS) tend to increase from Arizona and Mexico through South America, but clines could not be demonstrated because of high individual variability in this character. Many South American aeneus have small intergenials inserted deeply between the posterior chin shields. This condition is relatively rare from Colombia north. Mean ventral counts are highest in Arizona and Sonora, and lowest in the Santa Marta Mountains of Colombia, Ecuador, and Venezuela. Mean caudal counts tend to be lower in South America, but the high extremes shown by many southern aeneus equal or exceed the means for numerous Mexican and Central American samples. Dorsal scales in aeneus from all parts of the range are usually 17-17-13, with an increase to 14 or 15 or a decrease to 12 or 11 near the anus in some individuals. Seventy percent of the specimens from Mexico, Central America and South America have similar reduction patterns, but the mean ventral number for the first reduction drops slightly from north to south and the range of ventrals over which these reductions take place drops from 127 to 154 for Arizona and Mexico to 107 to 137 for South America.

Tooth counts revealed trends, but no differences of diagnostic importance. Modifications in the skull bones are associated mainly with snout proportions. The nasals and prefrontals tend to be longer in those populations having relatively longer snouts. Lateral processes of the premaxilla may be present or absent in samples from Mexico, Central America and South America. Few differences were noted in bones posterior to the snout region. Two adults from the Pearl Islands of Panama have unusually heavy quadrate bones, but this may possibly be credited to individual variation or increased ossification in older snakes.

Variation in hemipenial size and ornamentation is great in all parts of the range, but most striking in individuals from southern Zacatecas, Sinaloa, and the Tres Marías Islands. Males from these areas have hemipenes that are smaller in diameter with the basal spines reduced or absent. The tail bases are correspondingly reduced. No disruption in mean measurement clines and scale counts, or changes in coloration are associated with these populations. The situation is apparently one of morphological similarity in three geographically separated populations.

Color patterns are remarkably variable in most samples and individual differences in every detail are apparent. South American specimens exhibit a greater variety of ventral patterns than those from other parts of the range, although every pattern seen north of Colombia is represented on the southern continent. Dorsal coloration and patterns vary widely in all parts of the range, but all variations noted in South America, are also found in Central America and Mexico. Specimens from the Rio Ucayali drainage in eastern Perú have the chin shields and anterior throat regions mottled to varying degrees with black, but the degree to which this has been affected or caused by preservatives is not known. If this color is not an artifact, it may be diagnostic of an undescribed race.

With the exception of the Ucayali drainage aeneus just noted, individuals from one part of the range cannot be separated with any degree of assurance from those of other parts. Designation of subspecies at this time would be tenuous at best. On the basis of the available data, I therefore recognize *Oxybelis aeneus* as a wide-ranging monotypic species.

TABLE 1. Geographic variation in the number of maxillary teeth

Area	16	17	18	19	20	21	22	23	24	25	26	27
Arizona	-	-	1	2	7	1	-	-	-	-	-	-
Mexico, N.W. coast	-	-	6	15	27	4	-	-	1	-	-	-
Mexico, N.E. coast	2	6	6	-	-	-	-	-	-	-	-	-
Mexico, southern	2	6	22	24	3	1	-	-	-	-	-	-
Tres Marias Id.	-	-	-	-	-	-	5	4	-	1	-	-
British Honduras	-	-	2	1	-	-	-	-	-	-	-	-
Guatemala	-	1	8	6	-	-	-	-	-	-	-	-
Honduras	-	-	6	6	-	-	-	-	-	-	-	-
Bay Islands	-	1	8	10	3	-	-	-	-	-	-	-
El Salvador	-	-	3	-	-	-	-	-	-	-	-	-
Nicaragua	1	-	8	2	2	-	-	-	-	-	-	-
Corn Islands	-	-	4	-	-	-	-	-	-	-	-	-
Costa Rica	1	-	10	8	7	7	1	2	-	-	-	-
Panama	-	-	-	1	5	9	7	3	1	-	-	-
Colombia	-	-	8	5	-	1	2	12	2	-	-	-
Ecuador	-	-	-	-	-	-	2	7	1	3	-	1
Venezuela	-	3	4	17	4	-	-	-	-	-	-	-
Trinidad	-	1	2	6	-	-	-	-	-	-	-	-
Tobago	-	-	-	-	1	2	1	-	-	-	-	-
Guianas	-	-	1	8	4	6	6	1	-	-	-	-
Brazil, northern	-	-	1	2	6	2	3	4	1	-	-	-
Ceara-Pernambuco	-	2	1	1	-	-	-	-	-	-	-	-
Bahia	-	1	4	2	2	-	-	-	-	-	-	-
southeastern	-	-	3	-	2	-	-	-	-	-	-	-
Mato Grosso	-	-	3	1	-	-	-	1	-	-	-	-
Bolivia	-	-	2	1	4	9	3	1	-	-	-	-
Peru, Dept. Loreto	-	-	-	-	-	1	1	7	1	3	-	-
Peru, Bellavista	-	2	-	-	-	-	-	-	-	-	-	-
Total	6	23	113	118	77	43	31	42	7	7	0	1

TABLE 2. Variation in the number of palatine teeth

Region	9	10	11	12	13	14	15	16	Total
Mexico	-	2	10	7	6	2	2	2	31
Central America	-	-	2	2	7	8	3	-	22
South America	1	1	5	2	4	1	4	-	18
Total	1	3	17	11	17	11	9	2	71

TABLE 3. Variation in the number of pterygoid teeth

Region	6	7	8	9	10	11	12	13	14	Total
Mexico	3	-	5	5	8	9	1	-	-	31
Central America	-	-	-	3	2	12	1	1	3	22
South America	-	1	-	-	9	4	2	2	-	18
Total	3	1	5	8	19	25	4	3	3	71

TABLE 4. Variation in the number of dentary teeth

Region	18	19	20	21	22	23	24	25	26	27	28	29	Total
Mexico	3	2	4	4	7	6	3	-	-	-	-	-	29
Central America	-	-	-	5	3	10	4	-	-	-	-	-	22
South America	-	-	-	2	3	3	2	2	-	-	2	4	18
Total	3	2	4	11	13	19	9	2	-	-	2	4	69

TABLE 5. Variation in the number of temporal scales

Region	Anterior						Posterior								
	1-1	1-2	2-2	2-3	3-3	3-4	0-0	1-1	1-2	1-3	2-2	2-3	2-4	3-3	3-4
Arizona and Mexico	390	10	5	0	1	0	0	7	3	1	389	3	2	0	1
Central America	424	11	8	0	0	0	1	1	8	0	428	4	0	1	0
South America	312	6	6	1	1	1	0	1	2	0	322	1	0	0	1
Total	1126	27	19	1	2	1	1	9	13	1	1139	8	2	1	2

TABLE 6. Preocular and postocular variation

Region	Preoculars			Postoculars					Total Specimens
	1-1	1-2	2-2	1-1	1-2	2-2	2-3	3-3	
Arizona and Mexico	406	4	1	5	7	398	1	-	411
Central America	442	-	1	3	1	434	4	1	443
South America	326	1	-	5	2	319	1	-	327
Total	1174	5	2	13	10	1151	6	1	1181

TABLE 7. Geographic variation in the number of supralabials

Area	6-6	6-7	7-7	7-8	7-9	8-8	8-9	8-10	9-9	9-10	10-10	Total
Arizona	-	-	-	-	-	5	1	1	2	-	-	9
Mexico, Sonora	-	-	-	-	-	8	12	1	13	-	-	34
Sinaloa	-	-	-	2	1	24	11	-	7	3	1	49
Nayarit to Guerrero	-	-	-	10	1	45	31	-	26	5	1	119
Tres Marias Islands	-	-	-	-	1	7	2	-	1	-	-	11
Mexico, northeastern	-	-	-	-	1	4	8	-	6	-	-	19
Yucatan, British Honduras and N.E. Guatemala	-	-	1	2	1	48	7	1	3	1	-	64
Mexico, southern	-	-	-	1	-	26	9	2	75	15	2	130
Guatemala, southwestern	-	-	-	1	-	3	4	-	25	1	-	34
Honduras to Costa Rica	1	-	-	-	-	22	9	-	90	12	2	136
Bay Islands	-	-	-	-	1	2	2	1	25	3	3	37
Corn Islands	-	-	-	-	-	-	-	-	22	2	-	24
Panama	-	1	4	3	-	92	39	-	32	13	4	188
Colombia, northcentral	-	-	-	-	-	4	7	-	14	3	1	29
Colombia, Santa Marta Mts.	-	-	-	-	-	-	1	-	9	-	-	10
Colombia, western coast	-	-	-	-	-	7	-	-	-	-	-	7
Ecuador	-	1	2	1	-	7	2	-	2	-	-	15
Peru, northeastern	-	-	-	-	-	-	1	-	-	-	-	1
Venezuela, Maracaibo Basin	-	-	-	-	1	1	2	-	11	1	-	16
Venezuela, other	-	-	1	-	-	29	7	2	2	1	-	42
Trinidad	-	-	1	5	1	23	7	-	1	-	-	38
Tobago	-	-	-	-	-	2	2	-	1	-	-	5
Guianas	-	1	-	2	-	16	13	-	30	5	3	70
Brazil	-	-	-	2	-	6	18	-	56	15	1	98
Peru, Amazonas	-	-	-	-	-	3	2	-	10	-	-	15
Bolivia	-	-	1	-	-	4	7	-	22	1	2	37
Total	1	3	10	29	8	388	204	8	485	81	20	1237

TABLE 8. Variation in the number of supralabials entering orbit

Region	45/45	456/45	56/45	456/345	456/456	456/567	456/56	56/56	567/45	567/56	567/567	Other	Total
Arizona and Mexico	1	20	1	2	320	51	1	-	2	1	10	2	411
Central America	5	8	1	4	361	46	1	2	-	-	13	2	443
Colombia	2	1	-	-	36	1	1	-	-	-	3	2	46
Ecuador	2	1	-	-	10	1	-	-	-	-	1	1	16
Peru	-	-	-	1	14	-	1	-	-	-	-	-	16
Bolivia	2	7	1	-	21	2	2	-	-	-	2	1	38
Brazil	1	4	2	-	28	6	2	1	-	-	-	3	47
Guianas	16	10	4	1	24	5	3	3	-	-	2	3	71
Venezuela, Maracaibo Basin	-	-	2	-	4	2	1	4	-	-	-	-	13
Venezuela, Other	28	3	2	-	4	1	-	1	3	-	-	1	43
Trinidad	25	4	2	-	2	-	-	1	-	-	-	-	34
Tobago	1	1	1	-	2	-	-	-	-	-	-	-	5
Total	83	59	16	8	826	115	12	12	5	1	31	15	1183

TABLE 9. Geographic variation in the number of infralabials

Region	6-7	7-7	7-8	7-9	8-8	8-9	9-9	9-10	10-10	10-11	8-10	9-11	Total
Arizona and Mexico	-	-	2	-	28	31	267	50	29	2	-	2	411
Central America (excluding Panama)	-	-	1	-	16	21	177	29	7	1	-	3	255
Panama	2	12	1	4	51	35	58	9	8	-	-	-	180
Colombia	1	1	2	-	12	8	16	3	1	-	1	1	46
Ecuador	-	3	1	-	4	1	4	1	-	-	1	-	15
Peru	-	1	-	1	3	4	6	1	-	-	-	-	16
Bolivia	-	-	3	1	4	8	21	1	-	-	-	-	38
Brazil	-	2	3	3	14	15	40	12	7	1	2	-	99
Guianas	-	3	8	3	11	14	31	1	-	-	-	-	71
Venezuela	1	3	8	-	15	12	16	2	1	-	-	-	58
Trinidad	-	1	4	-	12	9	8	-	-	-	-	-	34
Tobago	-	-	-	-	2	1	2	-	-	-	-	-	5
Total	4	26	33	12	172	159	646	109	53	4	4	6	1228

TABLE 10. Variation in the number of infralabials contacting the anterior chin shields

Region	3-3	3-4	4-4	4-5	5-5	Other	Total
Arizona and Mexico	2	4	278	80	43	4	411
Central America (excluding Panama)	1	1	149	56	39	9	255
Panama	-	5	94	46	44	-	189
South America	3	9	182	70	53	10	327
Total	6	19	703	252	179	23	1182

TABLE 11. <u>Geographic variation in the chin shield ratios</u> (ACS/PCS)*

Region	$\bar{x}$	Max.	Min.	n	SD	CV	CD
Arizona and Mexico	0.612	0.782	0.468	85	0.071	11.573	.026
Central America	0.631	0.796	0.492	100	0.073	11.553	.026
South America	0.690	1.019	0.524	72	0.098	14.247	.048

*Sub-adults with head lengths (Hl) below 22.0 are excluded from sample.

TABLE 12. Geographic variation in the number of ventrals

Region	Males $\bar{x}$	Males Min.	Males Max.	Males n	Females $\bar{x}$	Females Min.	Females Max.	Females n
Arizona	194.0	192	197	6	199.0	196	201	3
Mexico, Sonora	194.5	188	201	16	197.2	193	204	14
Sinaloa	186.4	179	197	24	189.8	182	197	33
Nayarit to Jalisco	188.4	186	192	5	188.5	184	193	11
Michoacan to Guerrero	191.2	178	193	35	190.8	184	200	72
Tres Marias Islands	192.5	191	194	2	193.8	192	196	4
Mexico, northeastern	185.8	183	189	4	186.4	183	190	9
Oaxaca and S. Veracruz	189.5	181	197	31	190.4	182	197	65
Chiapas and Tabasco	183.0	175	192	8	183.7	177	193	29
Yucatan	189.1	180	195	16	192.6	188	197	20
British Honduras	188.5	187	190	2	191.7	186	195	9
Guatemala, northeastern	189.0	187	190	4	190.0	185	194	4
Guatemala, southern	182.4	175	193	15	186.5	177	199	17
Honduras	184.2	176	189	12	187.0	180	195	12
Bay Islands	189.4	186	194	21	191.9	181	198	17
El Salvador	-	-	-	0	184.7	181	189	6
Nicaragua	184.2	178	193	15	185.6	181	189	12
Corn Islands	189.1	183	197	14	192.8	190	192	9
Costa Rica	184.0	177	194	28	184.1	176	190	25
Panama	183.8	176	191	67	185.5	176	196	98
Colombia, southwestern	189.0	179	194	5	190.0	187	193	2
Colombia, northcentral	184.2	178	189	8	183.7	175	192	17
Santa Marta Mts.	178.0	173	184	5	183.3	178	189	4
Ecuador	182.5	177	188	2	179.9	173	184	11
Venezuela, Maracaibo Basin	178.6	174	181	5	181.4	177	186	11
Venezuela, northeastern	179.3	168	186	15	182.7	174	192	16
Venezuela, Amazonas	182.4	175	194	4	182.0	175	191	8
Trinidad	185.6	181	192	11	185.3	179	191	23
Tobago	185.5	185	186	2	192.5	191	194	2
Guianas	185.3	174	195	37	187.3	175	202	33
Brazil, Amazon Basin	188.8	179	197	12	192.1	184	203	20
Ceara-Pernambuco	191.3	184	205	8	190.0	190	190	1
Bahia	187.8	179	197	5	190.1	183	199	6
southeastern coast	187.1	180	192	13	192.3	185	200	22
Mato Grosso	187.3	182	195	3	190.0	186	194	6
Peru, Dept. Loreto	190.8	186	194	5	192.8	187	198	7
Peru, Bellavista	183.0	183	183	1	177.0	177	177	1
Bolivia	184.7	180	190	17	188.2	183	194	16

TABLE 13. Geographic variation in the number of caudals

Region	Males				Females			
	$\bar{x}$	Min.	Max.	n	$\bar{x}$	Min.	Max.	n
Arizona	176.0	170	183	4	169.0	162	171	2
Mexico, Sonora	185.4	182	192	6	178.1	173	183	8
Sinaloa	172.4	168	181	10	175.2	165	183	9
Nayarit to Jalisco	186.5	184	189	2	175.5	167	184	2
Michoacan to Guerrero	186.0	178	198	19	180.1	169	191	42
Tres Marias Islands	191.0	191	191	1	-	-	-	0
Mexico, northeastern	172.6	169	178	2	167.0	165	169	5
Oaxaca and S. Veracruz	176.9	152	187	21	174.5	160	188	29
Chiapas and Tabasco	179.0	166	192	5	168.8	163	175	7
Yucatan	191.5	184	197	12	186.7	181	196	9
British Honduras	189.6	186	196	3	180.2	178	182	4
Guatemala, northeastern	187.0	185	189	2	187.0	182	192	3
Guatemala, southern	178.6	162	203	9	170.9	158	198	10
Honduras	185.8	177	197	5	173.2	166	182	5
Bay Islands	186.2	176	193	10	186.0	183	190	5
El Salvador	-	-	-	0	163.0	158	167	4
Nicaragua	173.7	164	186	9	172.4	164	190	4
Corn Islands	180.1	176	184	3	168.8	161	174	5
Costa Rica	178.7	165	197	15	180.5	161	192	13
Panama	184.5	172	197	30	182.1	162	196	39
Colombia, southwestern	173.5	166	181	2	-	-	-	0
Colombia, northcentral	161.6	161	163	3	166.3	154	189	9
Santa Marta Mts.	160.5	155	167	4	164.3	153	171	3
Ecuador	-	-	-	0	179.3	177	181	3
Venezuela, Maracaibo Basin	-	-	-	0	160.5	151	168	5
Venezuela, northeastern	164.5	139	177	7	167.3	162	173	8
Venezuela, Amazonas	161.5	142	181	2	154.8	137	169	7
Trinidad	175.4	171	179	5	171.3	156	181	13
Tobago	-	-	-	0	173.0	173	173	2
Brazil, Amazon Basin	167.5	154	188	12	168.2	146	184	15
Ceara-Pernambuco	161.8	153	174	5	158.0	158	158	1
Bahia	165.0	159	173	4	165.5	162	168	4
Southeastern Coast	166.8	161	174	11	169.3	161	178	18
Mato Grosso	166.3	157	178	3	154.6	144	161	3
Peru, Dept. Loreto	171.4	169	177	4	171.5	162	180	4
Peru, Bellavista	-	-	-	0	154.0	154	154	1
Bolivia	165.0	158	178	12	159.8	148	171	13

TABLE 14. Summary of geographic variation in eye diameter/snout length (E/Sl) and eye diameter/internasal length (E/INl)

Region	Means of Ratios				% of Adults[1] with E/IN over 1.00	n[2]
	E/Sl		E/INl			
Arizona	0.298		0.806		00.0	9
Mexico, Sonora	0.316		0.846		00.0	27
Sinaloa	0.321		0.896		09.5	44
Nayarit to Jalisco	0.339		0.941		15.3	15
Tres Marias Islands	0.339		0.904		16.6	6
Michoacan to Guerrero		0.312		0.879	07.1	68
Mexico, northeastern	0.328		0.908		06.2	14-16
Oaxaca and S. Veracruz	0.329		0.911		06.4	75-83
Yucatan	0.343		0.971		51.8	27-30
Chiapas and Tabasco	0.351		1.022		70.0	17-20
Guatemala, northeastern	0.352		0.971		50.0	10
British Honduras		0.386		1.041	62.5	8
Guatemala, southern	0.356		1.000		53.4	28-30
Honduras	0.364		1.074		70.5	17-18
Bay Islands	0.376		1.116		100.0	28-32
El Salvador	0.382		1.090		80.0	5-6
Nicaragua		0.356		1.055	74.0	25-27
Corn Islands		0.353		1.026	56.0	24-25
Costa Rica		0.370		1.052	74.0	39-49
Panama	0.398		1.185		98.5	125-145
Colombia, west coast	0.382		1.137		85.7	7
Ecuador, western	0.370		1.033		70.0	10
Colombia, northcentral		0.374		1.053	77.7	25-27
Santa Marta Mts.	0.382		1.063		100.0	7
Venezuela, Maracaibo Basin	0.357		0.977		40.0	10
Venezuela, northeastern	0.343		0.941		19.0	18-22
Venezuela, Amazonas	0.331		0.884		00.0	6
Trinidad		0.376		1.061	83.3	21-24
Tobago		0.380		1.038	50.0	4
Guianas	0.359		0.978		50.0	48-55
Brazil, Amazon Basin	0.361		0.986		50.0	12
Ceara-Pernambuco		0.331		0.950	20.0	5
Bahia		0.352		0.970	50.0	6
Southeastern coast		0.384		1.001	66.6	3
Mato Grosso	0.355		0.910		00.0	3
Peru, Dept. Loreto	0.345		0.921		16.6	6
Bolivia	0.341		0.910		15.6	30-32
Peru, Bellavista		0.363		1.118	100.0	3

[1]Adults are defined as specimens with head lengths (Hl) over 22.0 mm.

[2]Sample size for ratio means is variable because measurements could not be made on all individuals due to snout, eye or internasal scale distortions.

TABLE 15. Geographic summary of measurement ratios for Oxybelis aeneus with head lengths (Hl) of 22.0 mm or more

Ratio	Region	$\bar{x}$	Max.	Min.	n	S.D.	C.V.	C.D.
T/SV	Arizona and Mexico	0.686	0.777	0.574	158	0.034	4.988	0.281
	Central America	0.699	0.818	0.541	144	0.051	7.231	0.155
	South America	0.665	0.785	0.549	131	0.040	6.084	0.240
Hl/SV	Arizona and Mexico	0.038	0.045	0.033	348	0.020	4.862	0.278
	Central America	0.038	0.048	0.031	348	0.020	7.733	0.110
	South America	0.038	0.049	0.032	231	0.030	7.613	0.128
Sl/Hl	Arizona and Mexico	0.412	0.476	0.351	345	0.010	4.449	0.151
	Central America	0.390	0.474	0.339	354	0.020	5.061	0.029
	South America	0.401	0.480	0.319	245	0.023	5.668	0.156
Hw/Hl	Arizona and Mexico	0.270	0.401	0.198	342	0.033	12.344	0.023
	Central America	0.280	0.381	0.218	347	0.030	10.424	0.091
	South America	0.280	0.409	0.197	245	0.031	11.093	0.223
E/Hl	Arizona and Mexico	0.133	0.181	0.109	346	0.010	7.188	0.299
	Central America	0.147	0.197	0.113	351	0.013	9.143	0.147
	South America	0.144	0.183	0.107	248	0.011	7.456	0.227
E/Sl	Arizona and Mexico	0.325	0.453	0.254	338	0.028	8.706	0.145
	Central America	0.377	0.505	0.281	344	0.035	9.275	0.138
	South America	0.359	0.464	0.262	244	0.029	7.971	0.094
E/INl	Arizona and Mexico	0.904	1.250	0.673	333	0.083	9.236	0.065
	Central America	1.105	1.593	0.787	340	0.127	11.351	0.112
	South America	0.990	1.281	0.630	241	0.011	10.061	0.071
INl/Sl	Arizona and Mexico	0.359	0.463	0.298	328	0.022	6.193	0.093
	Central America	0.343	0.455	0.264	337	0.024	6.966	0.024
	South America	0.364	0.474	0.254	237	0.027	7.749	0.015
INl/Hl	Arizona and Mexico	0.148	0.185	0.110	335	0.010	6.503	0.209
	Central America	0.134	0.180	0.103	343	0.010	7.509	0.028
	South America	0.146	0.187	0.117	241	0.013	8.662	0.115
INw/Hl	Arizona and Mexico	0.113	0.136	0.073	294	0.090	7.941	0.062
	Central America	0.118	0.145	0.079	278	0.010	8.960	0.055
	South America	0.120	0.169	0.089	220	0.010	8.213	0.118
INw/INl	Arizona and Mexico	0.769	1.000	0.488	294	0.074	9.651	0.122
	Central America	0.888	1.185	0.655	277	0.088	9.874	0.034
	South America	0.825	1.194	0.595	220	0.084	10.168	0.032
Sn/Sl	Arizona and Mexico	0.135	0.226	0.017	257	0.031	22.732	0.188
	Central America	0.110	0.235	0.019	247	0.034	30.546	0.080
	South America	0.110	0.233	0.031	188	0.033	29.679	0.130
Hl'/Hl	Arizona and Mexico	0.791	0.948	0.647	345	0.026	3.344	0.228
	Central America	0.789	0.925	0.696	357	0.034	4.279	0.210
	South America	0.799	0.948	0.582	244	0.034	4.202	0.145

TABLE 16. Food of *Oxybelis aeneus* in nature

Food	Source
Insects (general)	Wagler (1824), Villa (1962)
Frogs (general)	Mole (1924), Rohl (1942, 1956), Beebe (1946), Wehekind (1955)
Hyla rubra	Beebe (1946)
Lizards (general)	Mole (1924), Barbour and Amaral (1926), Vorhies (1926), Ditmars (1928, 1945), Schmidt and Davis (1941), Rohl (1942, 1956), Stebbins (1954, 1966), Kennedy (1965), Santos (1955), Wehekind (1955), Wright and Wright (1957), Del Toro (1960), Villa (1962), Sexton, Heatwole and Meseth (1963), Fowlie (1965)
Anolis sp.	Del Toro (1960)
Anolis chrysolepis	Beebe (1946)
Sceloporus sp.	Schmidt (1928)
Sceloporus consobrinus	Barbour and Amaral (1926)
Uta ornata	Bogert and Oliver (1945), Stebbins (1954)
Holbrookia maculata	Stebbins (1954)
Ctenosaurus hemilopha	Stebbins (1954)
Gymnophthalmus sumichrasti	Schmidt (1928)
Gymnophthalmus speciosus	Smith and Grant (1958)
Cnemidophorus lemniscatus	Smith and Grant (1958)
Cnemidophorus deppei	Stuart (1954b)
Ameiva sp.	Beebe (1946)
Basiliscus basiliscus	Netting (1936)
Birds (general)	Mole (1924), Rohl (1942, 1956), Beebe (1946), Santos (1955), Wehekind (1955)
female manakin	Beebe (1946)
Mammals	
rodents	Villa (1962)

FIGURE 1. Distribution of Oxybelis aeneus in North America

● Locality records for specimens examined.

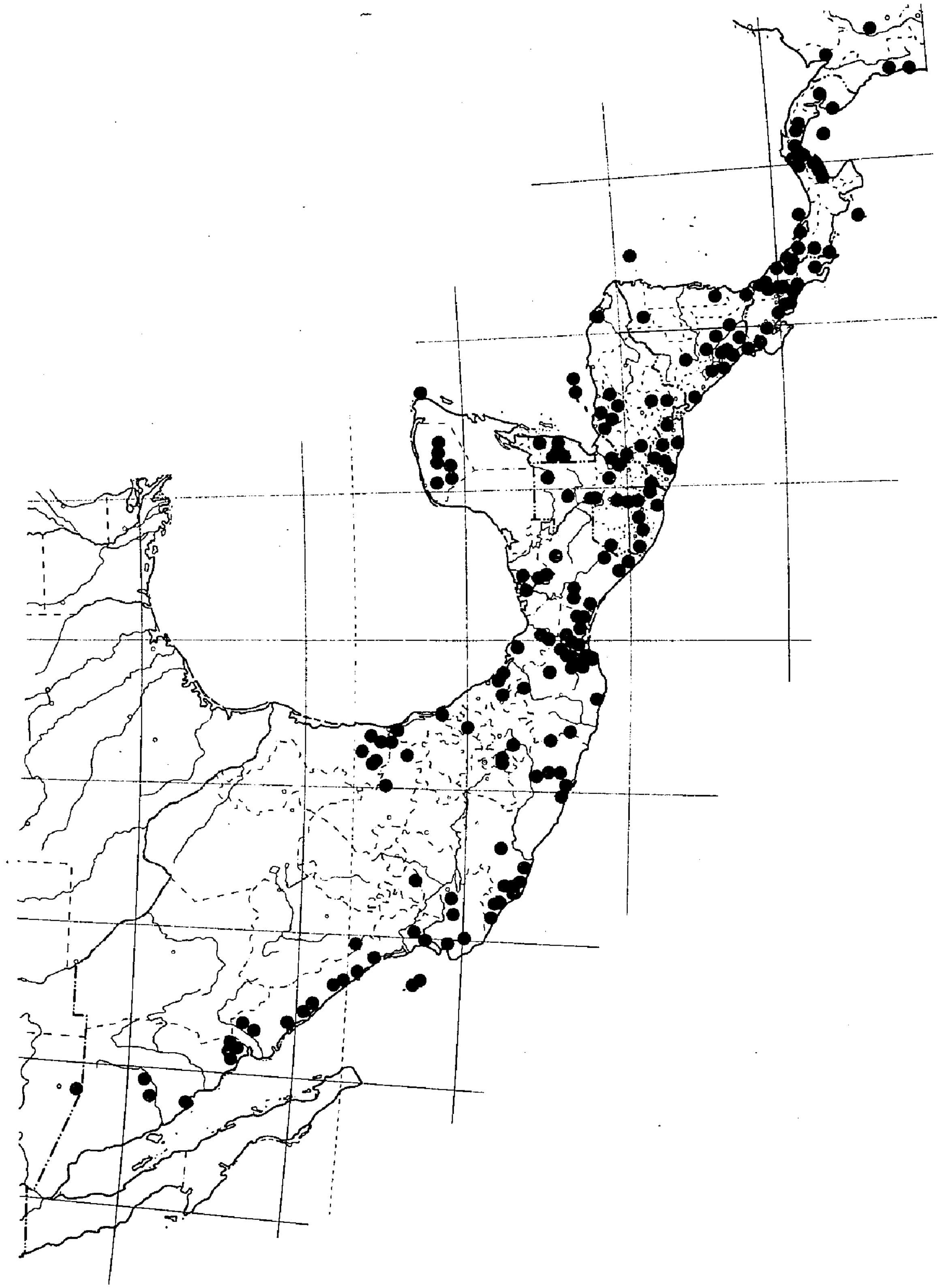


FIGURE 2. Distribution of *Oxybelis aeneus* in South America

● Locality records for specimens examined.

▲ Locality records for Instituto Butantan specimens.

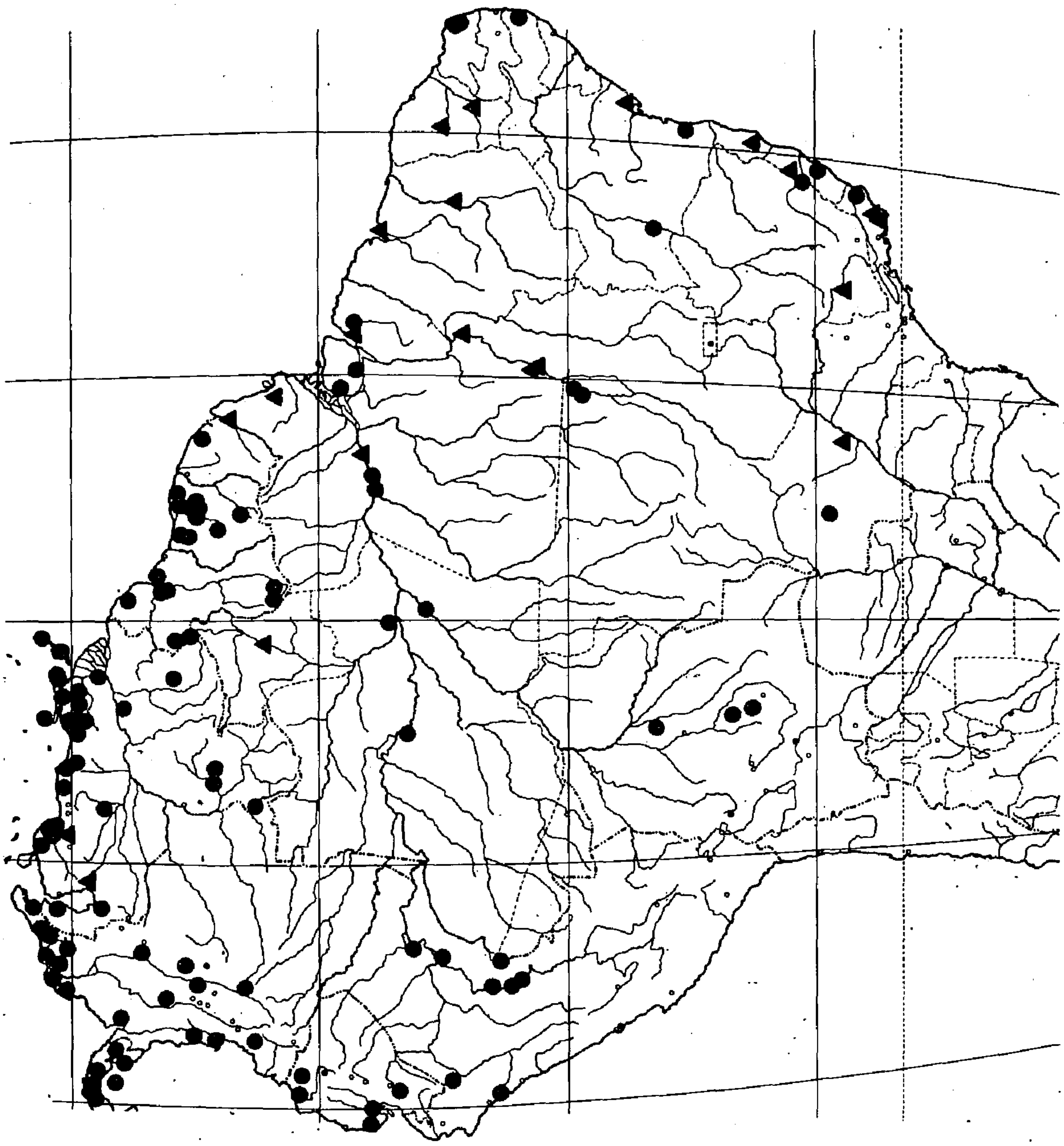


FIGURE 3. <u>Geographic variation in the shape of the prefrontal bones</u>

A. Mexico: Michoacan (28.6 mm), Sinaloa (29.7 mm), Sonora (32.0 mm), Tabasco (32.8 mm).

B. Mexico: Oaxaca (19.5 mm), (25.5 mm), (ca. 28.0 mm), (28.6 mm).

C. Mexico: Chiapas (16.0 mm), (18.1 mm), (23.0 mm), (28.6 mm).

D. Costa Rica (29.1 mm), (29.6 mm), (30.1 mm), (39.2 mm).

E. Colombia (?), Panama (25.6 mm), (30.9 mm), (36.1 mm).

F. Brazil (36.6 mm), Peru (28.2 mm), Ecuador (ca. 32.0 mm), Colombia (22.6 mm).

G. Trinidad (?), Venezuela (28.9 mm), Brazil (26.6 mm).

Note: The numbers in parentheses are the head lengths (Hl), of the specimens from which the bone drawings were made.

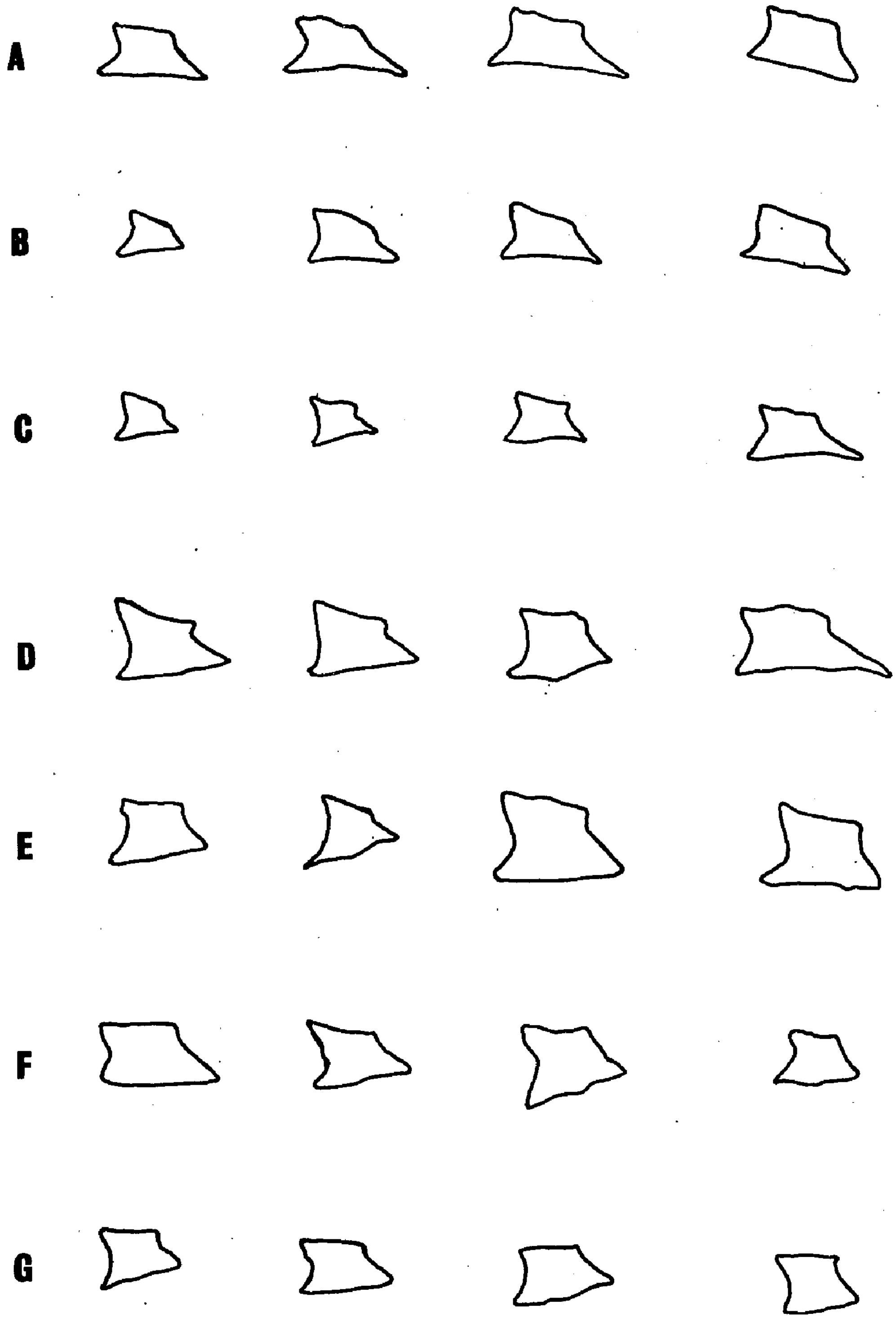

A
B
C
D
E
F
G

FIGURE 4. Geographic variation in the shape of the premaxilla

A. Mexico: Sonora (ca. 32.0 mm), Sinaloa (29.7 mm), (30.5 mm).

B. Mexico: Tabasco (32.8 mm), (34.0 mm), Michoacan (28.6 mm), Colima (32.1 mm).

C. Mexico: Chiapas (23.0 mm), (28.6 mm), Oaxaca (25.5 mm), (19.5 mm), (ca. 28.0 mm), (31.5 mm).

D. Nicaragua (ca. 34.0 mm), Costa Rica (29.6 mm), (30.1 mm), (39.2 mm).

E. Panama (25.6 mm), (30.9 mm), (33.5 mm), (36.1 mm).

F. Colombia (22.6 mm), Brazil (26.6 mm), (36.6 mm), Peru (28.2 mm), Ecuador (ca. 32.0 mm), Venezuela (28.9 mm).

Note: The numbers in parentheses are the head lengths (Hl), of the specimens from which the bones were drawn.

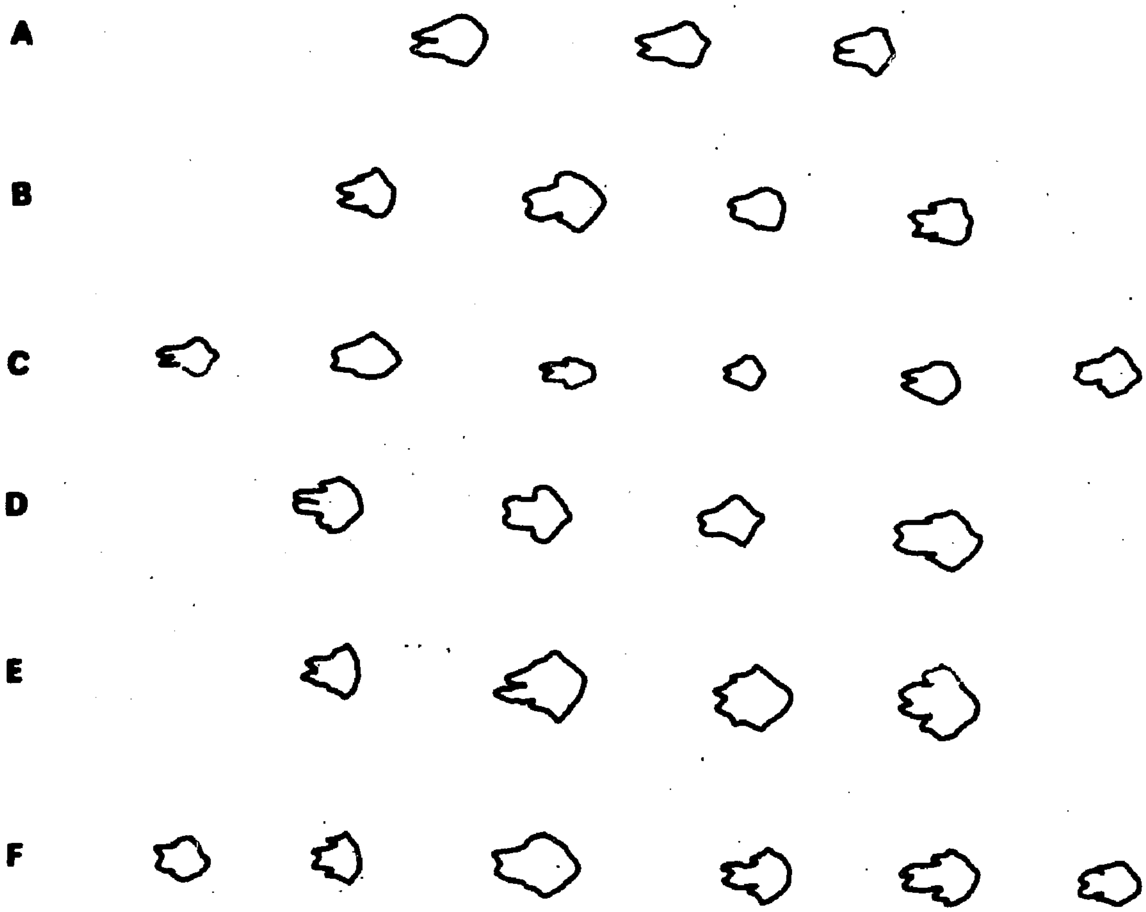

A
B
C
D
E
F

FIGURE 5. <u>Geographic variation in the shape of the nasal bones</u>

A. Mexico: Sonora (32.0 mm), Sinaloa (29.7 mm), (30.5 mm).

B. Mexico: Tabasco (32.8 mm), (34.0 mm), Michoacan (28.6 mm), Colima (32.1 mm).

C. Mexico: Oaxaca (19.5 mm), (25.5 mm), (ca. 28.0 mm).

D. Mexico: Chiapas (16.0 mm), (18.1 mm), (23.0 mm), (28.6 mm).

E. Costa Rica (29.1 mm), (29.6 mm), (30.1 mm), (39.2 mm).

F. Panama (17.4 mm), (25.6 mm), (30.9 mm), (33.5 mm), (36.1 mm).

G. Colombia (22.6 mm), (?).

H. Brazil (26.6 mm), (36.6 mm), Peru (28.2 mm), Venezuela (28.9 mm), Ecuador (ca. 32.0 mm).

Note: The numbers in parentheses are the head lengths (Hl), of the specimens from which the bones were drawn.

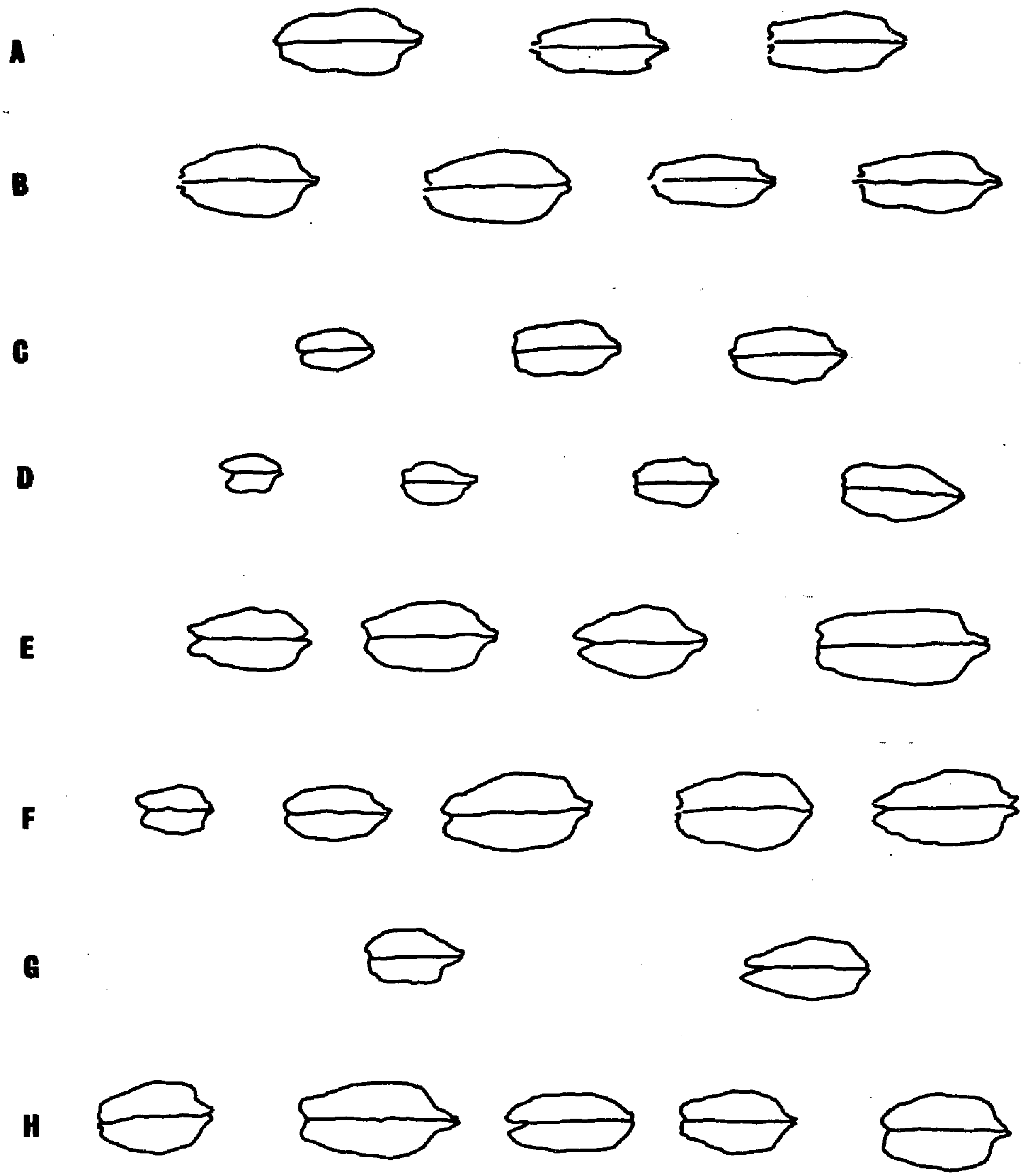
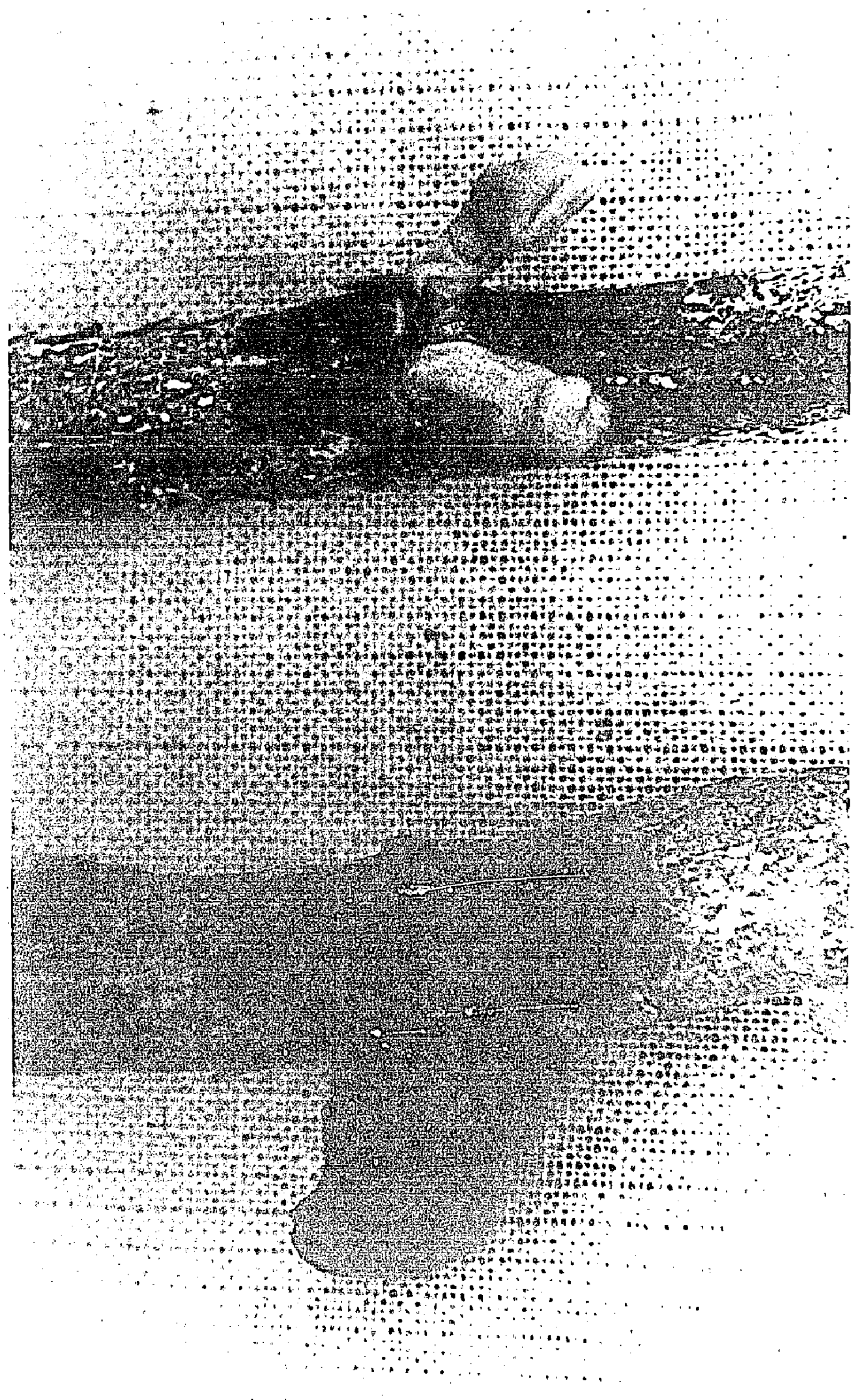

A
B
C
D
E
F
G
H

FIGURE 6. <u>Hemipenial differences in two Mexican</u> Oxybelis aeneus

Left: Large hemipenes with well-developed basal spines. The specimen is UMMZ 82656 from Oaxaca. The snout-vent length of this snake is 774.0 mm.

Right: Small hemipenes with reduced basal spines. The specimen is UK 73586 from Sinaloa. The snout-vent length of this snake is 774 mm.



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VITA

Edmund Davis Keiser, Jr., was born in Appalachia, Virginia, on February 18, 1934. He attended public schools in Appalachia, Virginia, Fulton, Kentucky, and Mt. Vernon, Illinois, graduating from Mt. Vernon Township High School in 1952. During the years 1952 to 1961, he attended Southern Illinois University, where he received the degree of Bachelor of Arts in 1956, and the degree of Master of Sciences in 1961. He entered the Graduate School of Louisiana State University in September, 1964. He is married to Patsy Ann Oswalt and they have one son. He is presently a candidate for the degree of Doctor of Philosophy in Vertebrate Zoology.

EXAMINATION AND THESIS REPORT

Candidate: Edmund Davis Keiser, Jr.

Major Field: Zoology

Title of Thesis: A Monographic Study of the Neotropical Vine Snake, Oxybelis aeneus.

Approved:

Douglas A. Rossman

Major Professor and Chairman

Max Goodrich

Dean of the Graduate School

EXAMINING COMMITTEE:

W J Harman

George H Thomas

J H Roberts

Clell B. Causey

Date of Examination:

July 6, 1967